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ECOLOGY

ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

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ECOLOGY OF THE BURROWEED

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Marked vegetational changes have occurred on extensive areas of southwestern range lands in rather recent years. The most conspicuous of these has been the partial or total disappearance of many of the formerly abundant grasses and their replacement by shrubs or low trees, many of which have comparatively little value either as forage for livestock or for the retardation of erosion.

Few of the shrubs have spread more rapidly or more widely than the burroweed, *Aplopappus fruticosus* Blake. These plants have not only increased in number on the lower ranges where they had been present for some time, but have also invaded the upper, better grassed areas. This increase has caused much concern among cattlemen, who feel that the unpalatable weeds are crowding out perennial grasses and in this way ruining the ranges for profitable grazing. Because of the undesirability of the weeds they have recently been the subject of intensive study relative to developing methods for their eradication.

The ecology of burrowweeds has heretofore been touched on only incidentally and in connection with other investigations. Although several of the early ecological studies made in Arizona list the more abundant species, no reference to burrowweeds, either by description or name has been found in the literature before 1900. Because of this it seems safe to say that the weeds probably were not present on the ranges in appreciable numbers until about 30 years ago. From subsequent studies it seems that burrowweeds have invaded the upland ranges in rather recent years (Griffiths, '04) probably from adjacent river valleys (Griffiths, '10). This spread has been attributed by Griffiths to protection from fire and by Clements ('20) to overgrazing. Griffiths observed, however, that even on ranges protected from grazing the weeds were spreading rapidly.

¹ Maintained at Tucson, Arizona, by the United States Forest Service in cooperation with the University of Arizona.

Thornber ('10) noted for various areas around Tucson, that even under protection, burrowweeds had spread markedly during the preceding 3 to 7 years. Although it is possible that this spread was due to a deteriorated condition of the ranges prior to protection, various studies indicate that prevention of fires probably played a greater part in this increase than heavy grazing.

DESCRIPTION AND CLASSIFICATION

Burrowweeds are low shrubs, densely branched from near the base (fig. 1). The leaves are about an inch in length, oblong or spatulate-oblong in shape, and lobed or pinnately parted. The numerous yellow flowers are borne in small, dense, almost sessile heads. Mature plants on the open range are usually about a foot in height, although in better-watered habitats, as along irrigation ditches or roadsides they sometimes reach a height of 3 or 4 feet.

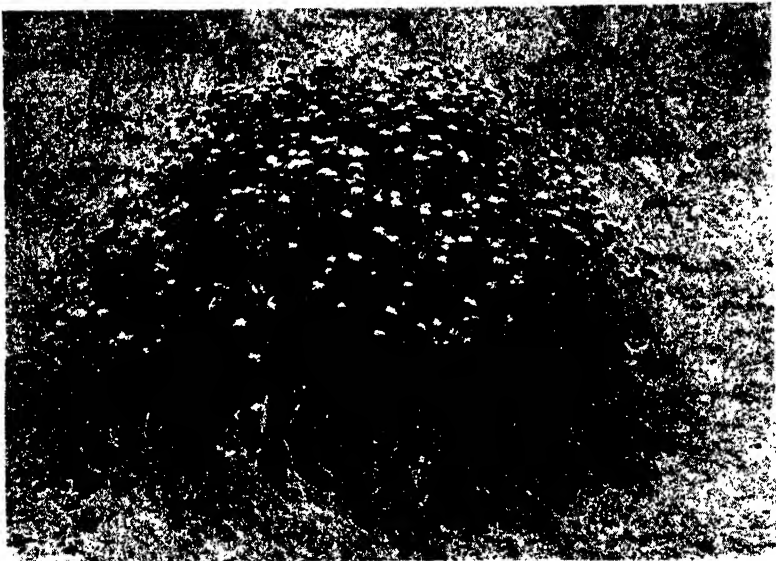


FIG. 1. Typical burrowweed plant about 2 feet high in full flower.

The genus *Aplopappus* is in the Aster tribe of the Compositae, the generic type (*A. glutinosus* Cassini) having been described in 1828. A reproduction of Cassini's original description is given by Hall ('28). Various species, now classed under *Aplopappus* were originally placed in other genera. As a result, the genus has a number of synonyms, the more common of which are *Chrysoma*, *Ericameria*, *Isocoma*, *Macronema*, *Pyrrocoma*, *Sideranthus*, *Stenotus*, and *Tonestus*. *Bigelovia* is a synonym in part. The species here studied, *Aplopappus fruticosus*, commonly known as burrowweed, but also misnamed rabbit brush, goldenbush, goldenweed, and rayless goldenrod, is frequently confused with its close relative, jimmyweed, *A. heterophyllus*.

HABITAT

Burroweeds are common on desert or semidesert areas throughout much of southwestern United States and northern Mexico. According to Hall ('28) they will grow on soils that contain a moderate amount of alkali. Inasmuch as they appear to thrive about as well on the fine alluvial soils of river valleys as on the coarser soils of outwash slopes, soil aeration or texture seem to affect their distribution little or not at all. They are, however, typically desert or semidesert plants and are not known to occur above the lower limits of the oak-juniper type of vegetation. On the outwash plains they are often most abundant at the same altitudes that support a good growth of grama grass, *Bouteloua rothrockii*. On the western foothills of the Santa Rita mountains they are abundant and conspicuous everywhere except locally near the extreme upper altitudinal limits (fig. 2). Above about 4,300 feet mem-



FIG. 2. Area on the Santa Rita Experimental Range badly infested with burroweeds. Mesquites formerly on the area have been removed.

bers of the somewhat woodier species, *Aplopappus laricifolius*, occur, but rather less abundantly than the burroweeds do below.

ECOLOGY

Seed germination occurs during the cool rainy winter or early spring months during a period of low temperatures and rather abundant soil moisture. Rather plentiful rainfall during January, February, and March and occasional showers during April, May, and June seem to provide optimum soil moisture conditions for germination and seedling establishment.

In 1935, although a large number of seedlings was noted on January 15, it seems probable that germination had occurred a few weeks earlier, inasmuch as the very young seedlings were difficult to distinguish from certain annuals that had appeared some time prior to the middle of January. Since germination tests made during the summer rainy season have not been successful, and since very young seedlings have never been observed on the range during this period it would seem that conditions for germination are favorable only during the winter.

It has been noted that maximum germination generally occurs on soils where a fairly heavy cover of annuals or a light stand of perennial grasses results in the accumulation of a fair amount of litter. On the other hand, germination is poor on areas under protection from livestock where much dead material from ungrazed grasses is allowed to accumulate. There is little or no germination on areas where erosion is so rapid as to prevent the establishment of a grass cover.

A study of the rate of seedling mortality throughout the year has shown that comparatively few seedlings survive from one year to the next. The results of this phase of the study are shown in table I. Here the number of

TABLE I. *Burroweed seedling mortality as related to precipitation*

Date	No. of seedlings	Rainfall, ¹ inches
April 4, 1934	309.8	
" 17	265.0	0.00
" 30	192.9	0.04
May 16	95.9	0.00
June 1	49.9	0.25
June 16	20.6	0.00
July 3	11.9	0.52
" 16	10.1	0.32
August 2	8.1	1.69
" 16	6.9	3.53
September 16	5.0	3.31
October 24	3.9	.92
December 4	3.7	.89
January 30, 1935	2.4	4.03
May 27	2.4	5.14

¹ Rainfall since the previous date noted.

seedlings represents the average that were present at periodic intervals on 10 one-meter quadrats. The rainfall record was obtained from a standard U. S. Weather Bureau gauge located near the quadrats.

Examination of the data contained in the table shows that the greatest seedling mortality occurred during the dry spring months that precede the summer rains. Root system studies have shown that during this period both burroweed roots and grass roots occupy approximately the same soil zones. Thus, it may be assumed that both burroweeds and grasses are dependent upon the same moisture supply, and that during the dry foresummer there probably is definite competition for the limited available moisture.

The data in table I show further that even though there is a reduction in the rate of seedling mortality with the beginning of the summer rains, a small percentage of the remaining plants die during the rather dry fall months. The decreased death rate upon the initiation of summer rainfall seems largely the result of an increase in available soil moisture. During the subsequent dry months prior to the first winter rains, the continued low mortality rate is probably due in part to the fact that most of the seedlings have already died, thus leaving more moisture for the remainder; in part to a less pronounced drought condition during the fall than during the spring months; and in part to the fact that the longer roots of the surviving seedlings penetrate to greater depths than most of the grass roots, and consequently are drawing upon a different moisture supply.

It has been found that fewer burroweed seedlings occur on protected areas with a good stand of grass than on grazed range where the grass cover is poor. The results of this phase of the study are shown in table II where the number of seedlings per square meter represents an average from 5 to 35 meter-square quadrats counted on the same number of quadrats on protected and grazed portions of each area.

TABLE II. *Relation between amount of grass and number of burroweed seedlings on grazed and protected range*

Study area	Grass density ¹		Seedlings per square meter	
	Grazed range	Protected range	Grazed range	Protected range
3C.....	9	10	25.5	7.9
7-26.....	4	15	24.8	6.9
7-28.....	4	16	24.8	6.9
7-25.....	4	16	24.8	6.9
7-27.....	4	17	24.8	6.9
7-17.....	19	26	24.8	6.9
1A-TP....	15	35	5.8	0.0
1A-CP....	19	39	27.8	1.9
37.....	4	11	25.4	3.7
Mean.....	9	20	23.2	5.3

¹ Per cent of the ground covered by perennial grasses.

Examination of the table shows that not only was the average grass density more than twice as high on the protected as on the grazed range, but that, in no instance, was the density as high under grazing as under protection. Similarly, the data show that there was an average of 23 seedlings on the grazed range to 5 on the protected, and that on every study area the seedlings were more numerous under grazing than under protection. The foregoing facts suggest that the relatively few seedlings present on protected

plots may be the result, directly or indirectly, of the heavier stand of grass there than on the grazed range.

Further investigations relative to burroweed seedling establishment have shown that although the weeds are numerous at the present time over most of the Santa Rita range, conditions for seedling survival are not equally favorable at all elevations. The number of seedlings at different elevations is given in table III.

TABLE III. *Relation between number of burroweed seedlings and altitude*

Altitude in feet	Seedlings ¹
3900-4000	3
3800-3900	4
3700-3800	14
3600-3700	7
3500-3600	26
3400-3500	51
3300-3400	22
3200-3300	11
3100-3200	2
3000-3100	0.28
2900-3000	0.35

¹ Counts made June 11, 1935.

The number of seedlings for each 100 foot change in elevation as given in table III was determined in the following manner: Seedlings were counted on meter-square areas every 25 paces apart on an approximately straight line extending from the upper altitudinal limit of burroweeds on the Santa Rita Experimental Range to the Santa Cruz river valley below the lower range boundary. The seedling number given for each altitudinal change of 100 feet represents an average of about 25 of these counts. Three other similar series of counts made on the range, together with miscellaneous observations, have served to corroborate the data contained in table III.

It will be noted that the greatest number of seedlings occurred between altitudes of 3400 and 3500 feet. This portion of the range is for the most part an area where annual grasses and mesquites, *Prosopis velutina*, are abundant and perennial grasses occur rather sparsely. This poor perennial grass cover and the fair amount of litter from annuals and mesquite leaves seem to provide rather ideal conditions for seedling establishment. The smaller number of seedlings above and below this elevation may be due, above, to greater competition from the better grass cover, and below, to so slight an accumulation of litter as largely to prevent seedling establishment.

Studies of the root systems of burroweed seedlings have shown that the young plants are well adapted for growth in regions where seasonally abundant rainfall is followed by drought. Root growth is extremely rapid where moisture is available, the roots penetrating vertically for the most part rather than horizontally. As shown in figure 3 *D* and *E*, taproots on two seedlings

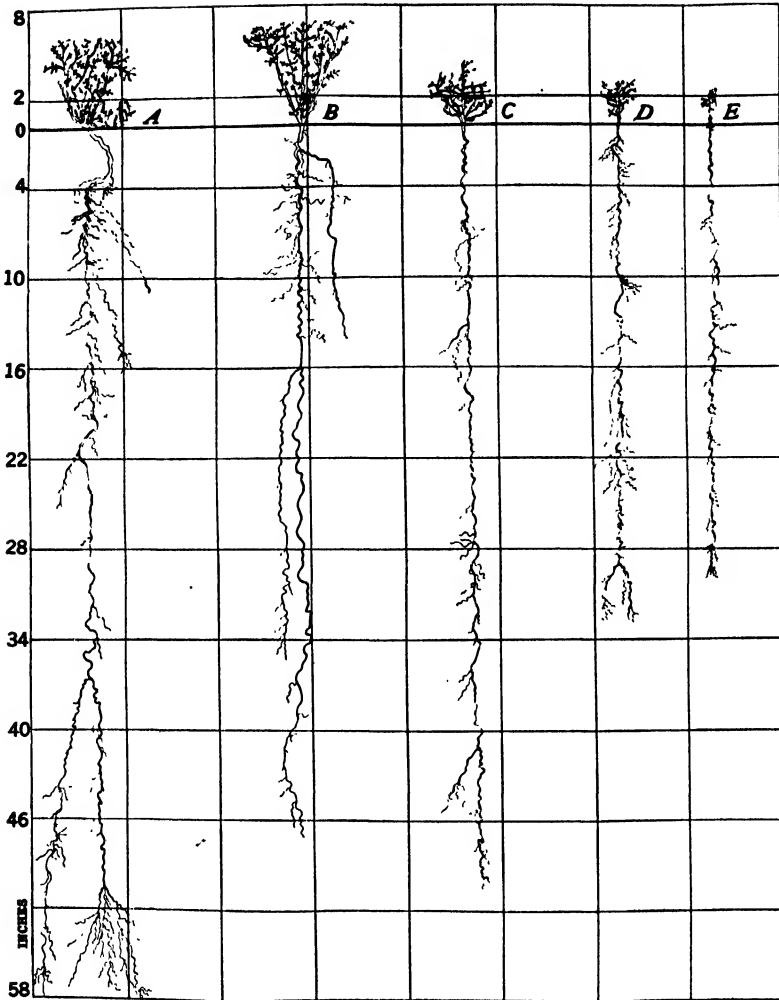


FIG. 3. The root systems of the burweed.

about 6 months old had an average length of 32 inches. The tops on these plants averaged 2.8 inches. Figure 3 shows further (*B* and *C*) that on two plants 18 months old the roots averaged 48.5 inches in length, while the tops averaged only 5.5 inches, and that a plant 2 years old (*A*) had a taproot 7 feet, 6 inches long and a top 7 inches high.

Root systems of mature burweeds, likewise, are well adapted for obtaining moisture in regions of low rainfall. Seven plants were excavated on the Santa Rita Range each of which had a long taproot from which a few lateral roots branched off near the soil surface. The length of these branch roots was not determined. The taproots, however, extended vertically for from 5 to

18 feet. Except for the branches near the soil surface there were almost no other side roots. From observations made on these and other excavated individuals it seems probable that most mature burroweeds growing on upland soils with a deep water table develop taproots 12 or more feet in length.

Little is definitely known of the causes responsible for the mortality of mature burroweed plants. It seems probable, however, that in the absence of fire, drought or physical injuries due to trampling or other influences are chiefly responsible for their death.

Burroweeds are parasitized by the grubs of 2 species of round-headed borers, *Crassidium intermedius* and *C. longipennis*, which live on the heartwood of the lower stems and roots. About 80 per cent of the mature plants have been found thus parasitized, and except for the fact that they may be somewhat more easily broken off than unaffected plants, they are apparently unharmed by the grubs.

The hollow stems and roots left by the borers are usually occupied by ants or termites which, in their turn, seem to do the plants little if any damage.

Two species of grasshoppers, *Taeniapoda eques* and *Hesperotettix viridis viridis*, are common on burroweeds during the summer, and, although they subsist on the leaves, have not been observed eating a sufficient portion of any of the plants to be harmful.

The age usually reached by mature burroweeds is not definitely known. It might seem that, inasmuch as the plants have hard, woody stems, their age could be determined by counting the annual rings. However, although the rings are present, they do not seem to be "annual" in all instances and are in addition often indefinite and sometimes impossible to distinguish; consequently, it is felt that they are an unreliable criterion of age. On the other hand, the general appearance of the weeds and the amount of soil retained by them under conditions of accelerated erosion, indicate that they often live for many years, possibly from 15 to 20.

Burroweeds are usually 18 to 24 months old when the first flowers appear. This blossoming usually begins late in the summer rainy period and continues until well into the fall. As seed maturation occurs from two to three weeks after the flowers open, it is evident that they are being produced during most of the flowering season. As a consequence of the rather long flowering period and the relatively short time required for ripening, large quantities of seeds are usually formed.

In spite of the fact that moisture conditions are usually good during the spring months, and that vegetative growth is active at this time, flowering does not occur until after the early summer drought has been broken by the summer rains. It was observed in the summer of 1934 that the weeds were flowering rather generally by August 1, while the following year they did not reach the same stage of flowering until about five weeks later. Yet the summer rains in 1934 were definitely subnormal, while those of 1935 were considerably

above average and began a week earlier than in 1934. It has been suggested that this apparent anomaly is normal and to be expected inasmuch as drought conditions are often required to initiate flower formation, although the embryonic flowers complete their development only as a result of subsequent rainfall. This phenomenon is in need of further basic physiological studies.

Although wind disseminated, the seeds are rather heavy for the amount of pappus and are usually not carried far, tending to accumulate in large numbers in the vicinity of and beneath burroweeds or other vegetation. It is probable that the large number of seedlings present in vegetative litter is in part the result of the retarding influence exerted by this litter on wind movement and wind disseminated seeds.

Recent studies have shown that on areas where protection from grazing resulted in a good stand of grass there were fewer mature burroweeds than on areas not so protected. The reason for this control seems due in large part to the fact (as shown in table II of this paper) that relatively few burroweed seedlings become established where a good cover of grass is present.

Subsequent investigation has shown that although the weeds can be eradicated by torch-burning, acid-spraying, and grubbing, these methods are not practicable on the low-value range lands where burroweeds usually occur. The same study has indicated that broadcast burning may have some possibilities as an eradication measure on areas that will support a cover of perennial grasses when not overgrazed, although this needs further investigation.

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THE RELATION BETWEEN NORMAL RANGE AND MORTALITY OF FISHES DUE TO COLD AT SANIBEL ISLAND, FLORIDA

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Between 1886 and 1936 nine "freezes" or sudden lowerings of air temperatures due to cold waves from the north have occurred in the region of Sanibel Island, Florida. An analysis by Storey and Gudger ('36) of these freezes and the resultant destruction to fishes has shown that in this locality at least the most important factors are amount of fall, minimum temperature attained and the duration of the cold; but that various conditions such as velocity and direction of the wind and stage and range of the tide may profoundly modify the effects of the temperature conditions.

It seemed worth while to analyze the ranges of the fishes affected to determine whether, other factors aside, there is any clear relation between the range of a fish and its mortality due to cold at Sanibel. In other words, do fishes whose centers of abundance lie north of Sanibel suffer appreciably less during freezes than those with a more truly tropical range? Available data have been compiled into tables I, II and III in an attempt to answer this question.

It was not always easy and in some cases it was impossible to assign an exact range to a fish in Atlantic waters. The southern, eastern and western limits seemed comparatively unimportant to this study but are included for completeness. An average of authors' opinions gives a fairly reasonable center of abundance. The northern limits are complicated by the Gulf Stream, for a few and often numerous subtropical and even tropical fishes may be borne north during the summer and early fall, to turn up accidentally, but in some species regularly, near such points as Cape Hatteras, Cape Cod or along Nova Scotia; whereupon, though the fishes perish in the first cold of winter, they leave observers with no recourse but to extend ranges far beyond normal limits.

The northern limit of abundance in winter, the most difficult to ascertain, was particularly desired for comparison with the mortality at Sanibel, for of course the freezes occur only in winter. Records of seasonal abundance proved helpful clues. Many species disappear during the winter months. It is notably easier to establish the absence of a fish than it is to prove where it has gone. The movements of certain species have been worked out with care and accuracy. Some have been shown to migrate north and south for

considerable distances or between shallow and deeper water. But the actual whereabouts of a number of species during many months of the year is totally unknown.

Some of the information is contradictory. And "abundant" to one author may mean "not uncommon" to another, so these data must be carefully scrutinized and the training, ability, and opportunities of the author for observation must be considered in evaluating the material.

The fishes, omitting only those which have not been specifically identified, have been listed in three groups. Table I contains the *fishes always hurt* by freezes at Sanibel, table II those *fishes often hurt* and table III the *fishes seldom hurt*. The normal station of each species at Sanibel is included. "Deep" refers to depths over 15 feet, "medium" is 5-15 feet and "shallow" means less than 5 feet. These stations are approximate and relative and there is apt to be considerable overlapping. "Surface" and "pelagic" are self explanatory. Under "Seasonal abund records: north" an attempt has been made to bring together all available information direct or inferential on the winter habitat of each species. Seasonal records of rare occurrences north (Gulf Stream strays, etc.) are placed in the column of "Northern limits" along with the most northerly records. "Life zone" is the most general range classification. When a species ranges over more than one zone, that in which its center of abundance lies has been italicized.

The common names given are those in use at Sanibel. The numerals refer to months of the year. "Ga 1-5" means "Georgia, January to May." "Off Hatteras" refers to fishing grounds along the edge of the Gulf Stream which passes close to Cape Hatteras before it veers toward Iceland and Europe. Abbreviated references to the sources of information are put in parentheses. The complete citations are listed at the end of this paper.

Explanations of other abbreviations follow:

N.....north
E.....east
W.....west
S.....south
abun.....abundant
acc.....accidental
com.....common
irreg.....irregular
no rec.....no record
nr.....near
occ.....occasional
spec.....specimen
strag.....straggles
subtrop.....subtropical
temp.....temperate
trop.....tropical
unc.....uncommon
unk.....unknown
yrs.....years

Ala.....Alabama
BWI.....British West Indies
CB.....Chesapeake Bay
Fla.....Florida
Ga.....Georgia
Gulf.....Gulf of Mexico
LI.....Long Island, N. Y.
La.....Louisiana
Mass.....Massachusetts
Me.....Maine
Miss.....Mississippi
NC.....North Carolina
NJ.....New Jersey
NY.....New York
SC.....South Carolina
SHB.....Sandy Hook Bay
US.....United States

TABLE I. Ranges of fishes always hurt during freezes at Sanibel (abbreviations on page 11)

Species	Normal Sanibel station	Range				Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north	Northern limits	
Tarpon <i>Tarpon atlanticus</i>	all depths	Brazil Panama (M&H23) Bermuda (T&BeanO6) unc Bermuda (B&TV33a)	Brazil to Gulf coast mostly Gulf of Mex (Br29) not unc Union I, BWI (B&H35) Texas (Fo31a)	visits NC seasonally (SO7)	rare Va 7 (Fo27b) rare NJ 8-9 (Fo25b) rare and irreg SHB; NY; NJ 7-9 (Br25) (B&R29) rare Orient, 1 spec in 30 yrs (Lath23) strag to Cap Cod (N&B27) (Br29) strag to Nova Scotia, 1 spec rec (B&W25) (H&S28)	trop and sub- trop
Eel, brown-spotted <i>Mystriophis interinctus</i>	shallow and med	West Indies no rec Bermuda (B&TV33a)	Gulf and West Indies	unk N of Fla	Pensacola (Br29)	trop and sub- trop
Gulf-top sail catfish <i>Felichthys felis</i>	med and deep	Trinidad (Metz19) Panama (M&H23) no rec Bermuda (B&TV33a)	south Atlantic and Gulf coasts not unc NC (SO7)	caught with market fishes: NC 5-11 (H&P27)	unc CB (H&S28) unc N of Del (Br29) rare NY (N13) to Cape Cod (H&S28) to Mass (SO7)	trop and sub- trop
Common catfish <i>Galeichthys milberis</i>	all depths	Texas (Br29) no rec West Indies, Bermuda	south Atlantic and Gulf coasts com Texas (Fo31a) NC (SO7)	caught with market fishes: NC 5-11 (H&P27)	unc N of Va (SO7) (Br29) rare strag Woods Hole 1887 (N&B27) to Cape Cod (Br29)	sub- trop
Silver mullet <i>Mugil curema</i>	shallow	Brazil Trinidad and Venezuela (Fo31b) Texas (Fo31a) Tortugas (ASP34) Bermuda (B&TV33a)	Gulf and West Indies more S than <i>M. cephalus</i> (Br29) abun Puerto Rico (E&MO2)	com summer NJ (Fo25b) (Fo26b) com SHB: NY 8-11 (N13) (Br26) (N&B27) com Orient 6-12 (Lath17) (N&B27) com Woods Hole 7-10 (N&B27)	to Cape Cod (H&S28) (Br29)	trop and sub- trop

TABLE I.—Continued

Species	Normal Sanibel station	Range			Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north	
Amberjack <i>Seriola</i> sp.	pelagic	Brazil	West Indies Fla (H&C30) not unc La (Gun35) com Bermuda (B&TV33a) rare N of Fla (N&B27)	rare N of Fla	trop rare NC (SO7) rare CB (H&S28) rare summer NY; Woods Hole (N&B27) acc NY 7-8 (N13) strag to Mass (Br29)
Common jack <i>Caranx hippos</i>	surface and all depths	Brazil (Fo19) Panama (M&H25) Texas (Fo31a) unc Puerto Rico (E&MO2) no rec Bermuda (B&TV33a)	West Indies and Gulf warm waters (Br29) com NC, now unc Beaufort (SO7)	caught for market: NC 5-11 (H&P27) very young SHB 7 (Br26) fairly com NY 7-10 (N13) com NY; Orient 8-11 (N&B27) com Woods Hole 7-11 (N&B27)	trop and sub- trop unc NJ summer (Fo25b) unc Orient 7-10 (La17) rare summer Woods Hole (B&W25) to Cape Cod (N&B27) to Mass (Br29) strag Gulf of Maine (B&W25)
Blue runner <i>Caranx crysos</i>	surface and all depths	Brazil (N&B27) Trinidad (Fo31b) Union I, BWI (B&H35) Panama (M&H25) unc Puerto Rico (E&MO2) Bermuda (TBeanO6) unc Bermuda (B&TV33b)	Gulf and West Indies	caught for market: Fla 11-5 (F&M26) NC summer only, less com than <i>C. hippos</i> (SO7) not unc CB summer (H&S28) fairly com NY 7-10 (N13) com NY, Woods Hole, Orient 7-11 (N&B27)	trop and sub- trop irreg 10-11 Orient (La18) small spec Orient 7 (La20) rare large spec N (N20a) to Cape Cod (H&S28) to Cape Cod strag to Nova Scotia (B&W25) (N&B27) (Br29)
Permit <i>Trachinotus falcatius</i>	shallow	Brazil Panama (M&H25) S to Fla (JE&C30) unc Haiti (B&TV28) no rec Bermuda (B&TV33a)	Gulf and West Indies West Indies S (SO7) (H&S28) (Br29) com Puerto Rico (E&MO2) com Bahamas (BBeanO5)	rare N of Fla, summer only, mostly young	trop and sub- trop unc La (Gun35) rare NC, young (SO7) rare CB summer, young (H&S28) irreg, young SHB, NY 7-11 (N13) (Br25) (Br26) (N&B27) (Br28) (B&R29) (Br&N34) 2 recs Orient 9 (N&B27) rare Woods Hole 7-10 (N&B27) to Cape Cod (N&B27) (Br29) to Mass, young (H&S28)

TABLE II. *Ranges of fishes often hurt during freezes on Sanibel (Abbreviations on p. 11)*

Species	Normal Sanibel station	Range				Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north	Northern limits	
Ladyfish <i>Elops saurus</i>	surface	Brazil Panama (M&H23) Trinidad (Fo31b) 1 rec Bermuda (B&TV33a)	Gulf and West Indies Texas (Fo31a) unc N of NC (SO7) (Br29)	rare N of Fla	rare La (Gun35) irreg, unc SHB, NY 10 (N13) (Br24) (Br25) (Br28) (B&N34) Orient 10-11 (La17) (La20) Cape Cod (Br29) to Mass (SO7) (H&S28)	trop and sub- trop
Needlefish <i>Strongylura notata</i>	surface	Tortugas (ASP34) Fla Keys West Indies (BBeanO5) Puerto Rico (Fo28) Bahamas (BBeanO5) (Br34) no rec Bermuda (B&TV33a)	Fla Keys, West Indies, eastern Gulf coast	rare N of Fla	Pensacola (Br29)	trop and sub- trop
Hound minnow <i>Hyporhamphus unifasciatus</i>	surface	Brazil Trinidad (Fo31b) Panama (M&H23) Bermuda (TBeanO6)	Fla Keys and West Indies abund West Indies (Br29) (B&TV33a) Caribbean, Cuba, Bahamas (Br27) com N to Key West (JE&C30) com Bermuda (B&TV33a)	com CB summer (H&S28) com NY 8-10 (N&B27) com Orient 6-11 (N&B27) com Woods Hole 7-9 (N&B27)	unc NY 8-9 (N13) strag to Mass (H&S28) (Br29)	trop and sub- trop
Snake fish <i>Synodus foetens</i>	shallow and med	Brazil Panama (M&H23) Texas (Fo31a) Bermuda (TBeanO6) young com Haiti (B&TV28) unc Puerto Rico (E&MO2)	West Indies, Bermuda (B&TV33a) Bahamas, Cuba, British Honduras (Br27) com S of SC (JE&C30) abund NC (SO7) rare N of SC (Br29)	1 spec NJ 10 (Fo26b) many SHB 9 (Br31a) (Br32a) sometimes com NY 10 (N13)	rare strag NY 8-9 (N&B27) 1 spec Orient (La17) to Cape Cod (Br29) to Mass (SO7) (H&S28)	trop and sub- trop

TABLE II.—Continued

Species	Normal Sanibel station	Range				Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north	Northern limits	
Grunt, black or flannel mouth <i>Haemulon plumieri</i>	deep	Brazil Panama (M&H25) not unc Union I, BWI (B&H35) introduced Bermuda 1924 (B&TV33a)	Fla Keys and West Indies abund Hatteras to Brazil (JE&C30) com Haiti (B&TV28) com Bahamas (BBeanO5) West Indies to Hatteras (Br29) abund (offshore?) SC (SO7)		unc NC (SO7) strag N to SC; 1 spec CB (H&S28)	trop and sub- trop
Yellow jack; leather jack <i>Oligoplites saurus</i>	surface shallow and med	Curaçao and Trinidad (Metz19) Trinidad and Venezuela (Fo31b) Puerto Rico (E&MO2) (FoO5b) Haiti (Fo28) Haiti not abund (B&TV28) Tortugas (J&TO5) no rec Bahamas (BBeanO5) no rec Bermuda (TBeanO6) (B&TV33a)	tropical America (Br29) com Panama (M&H25) Central America and Indies (JE&C30) abund West Indies and Fla Keys (E&MO2) NC, Key West (FoO5b)		strag CB (H&S28) occ NY 8-10 (N13) rare NY 8-10 (N&B27) rare Woods Hole 8-9 (N&B27) NY, rarely Mass (Br29) no rec Gulf of Maine (B&W25)	trop and sub- trop
Sailor's choice; grunt <i>Oriopristis chrysopterus</i>	deep	Mexico (H&C30) Rio Grande (N&B27) Texas (Fo31a) no rec West Indies no rec Tortugas (J&TO5) (Gu29) Bermuda (TBeanO6)	south Atlantic and Gulf coasts (JE&C30) com Bermuda (B&TV33a) less com everywhere than form- erly (B&TV33a) unc N of Va (Br29)	NC 3-11; few off Hatteras 18 fathoms winter (H&C30) resident Beaufort (SO7) few, Va, fall (Fo27b) CB 4-10 (H&S28) scarce NJ summer (Fo26b) occ com NY 8-11 (N13) (N&B27)	irreg and rare 6-8 SHB (Br25) (Br26) (Br&N34) to NY (H&S28) young strag NY (JE&C30) rare Orient (Lal17) 1 spec Woods Hole (N&B27) to NY and Mass (Br29)	sub- trop and temp

TABLE II.—Continued

Species	Normal Sanibel station	Range			Life zone	
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north		
Angelfish, black <i>Chaetodipterus faber</i>	med and deep	Brazil Rio de Janeiro (N&B27) Trinidad (Fo31b) Panama (M&H28) Texas (Fo31a) introduced Bermuda (B&TV33a)	Gulf and West Indies southern Atlantic coast (JE&C30) com Haiti (B&TV28) rare N of CB (H&S28)	caught for market; NC 5-11 (H&P27) NC summer only (SO7) not unc CB 5-10 (H&S28)	rare and irreg NY & SHB 7-11 (N13) (Br25) (N&B27) (Br28) (H&S28) (B&R29) (Br31) (Br&N34) rare Orient (La17) to Cape Cod (N&B27) (H&S28) (Br29)	trop and sub- trop
Shark sucker <i>Echeneis remora</i>	all depths	Trinidad (Metz19)	warm seas (JE&C30) com Haiti (B&TV28) com Bermuda (B&TV33a) unc La (Gun35) few NC (SO7-quote Yarrow) rare CB (H&S28)	not unc NY, Woods Hole 7-10 (N&B27) not unc NY 7-8 (N13)	rare Orient (La19) Woods Hole (SO7) Cape Cod and Mass Bay strag (N&B27) unc Mass Bay (Br29) rare strag Gulf of Maine (B&W25)	trop and sub- trop
Toadfish <i>Opsanus tau</i>	shallow	Texas (Fo31a) rare Cuba (N&B27) no rec Bermuda (B&TV33a) no other recs West Indies	Cape Cod to Hatteras com La (Gun35) abun NC (SO7) spawns NY, NJ (Br31) permanent resident NY hibernates in mud first frost to April (N&B27)	caught with market fish; NC 5-11 (H&P27) Chincoteague, Va 5-10 (Fo27b) CB shallow summer, 5-27 fathoms winter (H&S28) abun NJ 8-9 (Fo25b) (Fo26b) resident NY (N13) (N&B27) com Block I 6-7 (Br32b)	to Cape Cod (N&B27) rare strag Gulf of Maine (B&W25) to Maine (Br29)	sub- trop and temp

TABLE III. Ranges of fishes seldom hurt during freezes at Sanibel (Abbreviations on p. 11)

Species	Normal Sanibel station	Range				Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north	Northern limits	
Mullet <i>Mugil cephalus</i>	shallow	Brazil (B&TV33a) Bermuda (TBean06) Haiti and Santo Domingo (Fo19) (B&TV35) no rec: Panama (M&H23) Puerto Rico (E&MO2)	Atlantic and Gulf (Br29) West Indies (B&TV33a) La (Gun35) Fla (F&M26) (Fi28) Bermuda (B&TV33a)	caught for market: Ga 1-5; Fla 11-4 (F&M26) NC 5-11 (SO7) (H&P27) CB 6-11 (H&S28) NJ summer (Fo26b) NY 7-10; Orient fall; Woods Hole 6-10 (N&Br27) resident NY (N13) hibernate in mud NY (N13) (B&W25) (N&B27) (Br29) winter in deeper water, don't migrate (Hu21)	rare N of NY (Br29) to Cape Cod (H&S28) strag Gulf of Maine (B&W25) (N&B27)	trop and temp
Mackerel, spanish <i>Scomberomorus maculatus</i>	pelagic	Brazil (Br29) Panama (M&H23) Texas (Fo31a) unc Cuba, Jamaica, Puerto Rico (E&MO2) unc Bermuda (B&TV33a) rare or absent Cuba (B&TV33a)	Atlantic and Gulf abun Gulf and N to NC (SO7) (N&B27) (Br29) com Gulf (JE&C30) West Indies (B&TV33a)	caught for market: Ga 10-4; Fla 10-5; Ala 12-4 (F&M26) NC 5-11 (H&P27) CB 5-9; migrate along coast (H&S28) once abun CB (SO7) rather com NY 5-9 (N&B27) com NY 8-9 (N13) none NC winter (B&W25) 1 spec Va spring (Fo27b) unc NJ 8-9 (Fo25b)	a few, fall, Orient (La17) rare Orient 8-10; because the authority is (N&B27) rare Woods Hole 8-10 (N&B27) to Cape Ann; strags to Maine (Br29) strags to Maine (B&W25) (N&B27)	trop and temp

TABLE III.—Continued

Species	Normal Sanibel station	Range				Life zone
		Southern, eastern and western limits	Center of abundance	Seasonal abun records: north	Northern limits	
Pompano <i>Trachinotus carolinus</i>	shallow and med	rare Brazil; West Indies (N&B27) Trinidad (Fo31b) unc Puerto Rico (E&MO2) no rec: Panama (M&H25) Bermuda (B&TV33a)	Gulf coast and Fla (Br29) CB S (SO7) only young com N of Va (Br29)	caught for market: Ga 1-12; Fla 12-4; Ala 12-4 (F&M26) None NC 11-5 (H&P27) irreg and not abun NC summer (SO7) not unc 5-11 CB to Mass (H&S28) young N of Va com only in summer (Br29) fairly com NY 8-11 (N13) a few young NJ 8-10 (Fo25b) (Fo26b) irreg abun SHB summer (Br29) many small; few large SHB 8-11 (N&B27) (B&R29) (Br&N34) rare, young Orient 9-10 (La17) (N&B27) rare, young Woods Hole 7-10 (N&B27)	to Cape Cod (N&B27) (Br29)	trop and sub-trop
Bluefish <i>Pomatomus saltatrix</i>	pelagic	Argentina (Fo26a) Trinidad (Fo31b) Venezuela (Metz19) unc Bermuda (B&TV33a) not taken (by M&H25) at Panama no rec: Puerto Rico (E&MO2) Haiti and Santo Domingo (B&TV28) (B&TV35) West Indies (Metz19)	warm seas (Br29) east coast US (JE&C30) abun Gulf, specs run small Sanibel, 1-2 lbs	caught for market: Fla 11-5 (F&M26) NC 5-11 (H&P27) well off Hatteras 11-2 (P32) CB 3-11 (H&S28) a few Del 8-9 (Fo27c) Orient 6-11 (La17) (La19) abun NY 5-10 (N13) (N&B27) abun Orient 6-11 (N&B27) abun Woods Hole 5-10 (N&B27) leaves northern inshore waters in winter (B&W25)	unc Block I 6-7 (Br32b) strag irreg Penobscot Bay and Mt. Desert I., Me (B&W25) (N&B27)	trop and temp
Redfish <i>Sciaenops ocellatus</i>	shallow and med	Texas (Fo31a) no rec: Tortugas (J&TOS) (Gu29) West Indies Bermuda (B&TV33a)	Atlantic and Gulf rare N of Va (Br29) unc N of CB (SO7) unc of N NJ (H&S28)	caught for market: Fla 11-4 (F&M26) NC 5-11 (H&P27) well off Hatteras winter (P32) inshore all winter NC (SO7) CB 5-10 (H&S28) abun fall Chincoteague (Fo27b) migrate S in winter (W&B23)	rare NJ 8-9 (Fo25b) (Fo26b) not rare NJ 5-10 (N&B27) rare, almost unk SHB, NY 6-9 (Br26) (N&B27) rare NY 5-10 (N13) 1 rec Woods Hole (N&B27)	sub-trop and temp

TABLE III.—Continued

Species	Normal Sanibel station	Range			Life zone	
		Southern, eastern and western limits	Center of abundance	Seasonal abund records: north		
Trout, spotted <i>Cynoscion nebulosus</i>	all depths	Texas (N&B27) (Fo31a) no rec: Tortugas (J&T05) (Gu29) West Indies Bermuda (B&TV33a)	Atlantic and Gulf rare N of Va (JE&C30) rare N of CB (SO7) unc N of Del (Br29)	caught for market: NC, SC, Ga 11-3; Fla 11-4 (F&M26) NC 5-11 (H&P27) well off Hatteras 12 (P32) abun NC 10-5; school up in creeks and deep holes; also that they migrate (W&B23) must winter NC shallow water; caught winter Beaufort; 8-5 Cape Fear; may migrate offshore winter (SO7, quote R. E. Coker) CB 3-12 (H&S28)	Northern limits rare NJ 8-9 (Fo25b) (Fo26b) to NY (H&S28) very rare Orient, only 3 recs 6-7 (N&B27)	sub-trop and temp
Pinfish <i>Lagodon rhomboides</i>	all depths	Texas (Fo31a) Cuba (JE&C30) (N&B27) no other West Indian rec Bermuda (TBeanO6) Bermuda only 1 rec (B&TV33a)	Atlantic and Gulf (JE&C30) com Tortugas (J&T05) com S of Va (H&S28) abun NY to Pensacola (N&B27) unc N of Del (Br29)	caught for market: NC 5-11 (H&P27) NC all year (SO7) CB summer and fall, never abun (H&S28)	occ NY 8-11 (N13) young SHB 8-11 (N&B27) rare Orient 8-11 (N&B27) and few strag Orient summer and fall (La23) usually rare Woods Hole 6-10 (N&B27) to Cape Cod (Br29) strag to Mass (H&S28)	sub-trop and temp
Sheephead <i>Archosargus probatocephalus</i>	shallow and med	Texas (Fo31a) Texas and Fla Keys (JE&C30) unc Tortugas (J&T05) no rec Bermuda (B&TV33a)	Atlantic and Gulf (JE&C30) Fla Keys (N&B27) La abun (Gun35) never abun NC (SO7) unc nowadays CB (H&S28)	caught for market: Ga 10-2; Fla 11-5; Ala 12-3; Miss 12-3 (F&M26) NC 5-11 (H&P27) well off Hatteras 12 (P32) NC spring to fall (SO7) NJ offshore 12 fathoms, summer to 7 lbs. (Fo26b) summer only nr NY (N&B27)	rare NY 6-10 (N13) (N&B27) none Orient since 1904 (N&B27) rare Woods Hole 7-8 (N&B27) to Cape Cod (Br29) strag to Bay of Fundy (B&W25) (N&B27) (Br29)	sub-trop and temp

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Krassovsky ('26) showed that removal of seminal roots of wheat, rye, and barley decreased the yield of grain and lengthened the vegetative period. Removal of nodal roots hastened maturity. Gericke ('23) found that the number of tillers was reduced on root-pruned wheat. Bates ('34) found that soil acidity limited root development of *Trifolium repens*, and reduced the leaf size in proportion to the degree of restriction. Pruning the roots at a depth of 4 inches likewise restricted the size of the leaves.

Object and Procedure

Experiments in which the root system of Sudan grass, *Holcus sorghum sudanensis* (Piper) Hitch., was limited to certain depths by repeated pruning were performed to determine quantitatively the effect upon plant growth both above and below ground.

Galvanized iron containers 5 inches in diameter and 6 and 11 inches deep were used. They held 2.27 and 4.54 kg. of soil, respectively, when filled to within 1 inch of the top. A one-half inch layer of sand was placed over the soil, thus leaving one-half inch space for watering. All containers of the same dimensions held the same amount of soil by weight. The containers will be referred to according to the depth of soil within them as "5's" and "10's." The bottoms of the containers in which the plants were root-pruned consisted of wire screen of quarter-inch mesh. These containers were inserted into larger ones (extensions) 5.5 inches in diameter and 15 inches deep, which were first filled with soil to within 3 inches of the top. Each extension held 6.25 kg. of soil, a column one foot deep. After filling both container and extension, they were joined and sealed outside with plasticine.

The soil was a fertile loam that had been well mixed and screened and brought to an optimum water content of 34 per cent, based on dry weight. Sufficient soil was retained in large, covered, galvanized iron receptacles to refill the extensions from time to time after the soil and roots in them had been recovered. After growth was well started, water content of soil, lost through absorption and transpiration as determined by decrease in weight, was replenished daily.

The containers were placed on tables in a greenhouse in such a manner that the tops were equally illuminated. They were spaced about a foot apart at the beginning, but the distance was increased to two or more feet as the growing plants demanded more light. The greenhouse roof was white-washed in alternate strips to prevent overheating; the glass was removed from one end of the house and all ventilators and windows were kept open.

Fourteen containers with extensions were used in each series of 5's and 10's. Six of these were reserved as controls, and in eight the roots were pruned. When pruning was done, the containers were twisted to break the roots and then pulled from their extensions. The roots were then cut off with a knife at the wire-mesh bottom. In addition, six 5's and six 10's with-

out extensions and with solid bottoms were employed. In three of each of these the tops were clipped at a height of four inches at ten-day intervals and on the same day that the roots were pruned in the others. The other three containers in each series were not disturbed.

Sudan grass was planted on June 11. After germination the plants were thinned to 15 per container. When the plants in the 5's were 11 inches tall, four of the containers from the lot of eight were lifted from their extensions, the roots cut off, and the screen bottoms painted with a mixture consisting of 85 per cent paraffin and 15 per cent vaseline. The pruning was done at 7 A.M. The containers with root-pruned plants and the remaining 5's (20 in all) were brought to their original weight by adding water, and then retained to determine the transpiration losses for the day. At 5 P.M. the roots were pruned from the plants in the four remaining containers of this set of eight. Two of the containers with their extensions were removed from the set of eight at the end of the day to obtain the development of roots and tops. The remaining six that had been root-pruned were placed back on the table after their extensions had been emptied of soil and roots and refilled with the original weight of fresh, moist soil. The number of tillers per plant was determined at this time as well as the average leaf area. The dry weight of the tops and the volume and dry weight of the roots were ascertained in the two containers and their extensions that were emptied. Also the tops of the plants in three of the 5's with the solid bottoms were clipped and the dry weight determined.

Every ten days thereafter a similar procedure was followed, the plants in two other containers with extensions being used, until none remained. At the close of the first ten-day period, after the original root-pruning, two containers of controls with extensions were also emptied and the roots and tops recovered to obtain a standard for comparison of decreased growth due to pruning. On the morning of the day these were removed they too were root-pruned and their transpiration losses determined along with the rest of the previously root-pruned plants, and controls. This same procedure was followed with the series of 10's.

The soil was washed from the roots over a 2-mm. mesh screen. Root volume was determined by displacement of water in a small, cylindrical graduate after the water on the surface of the roots had been removed by gently pressing them between blotting papers. Weights were ascertained after drying 48 hours at 100° C.

Results

The roots of the 5-inch series were first pruned on June 29, 16 days after germination. The average height was 11 inches. The average dry weight of the tops per container was 2.34 grams, number of tillers 1.3, and leaf area 11.85 sq. in. The dry weight of roots per container was 0.39 gram, and 0.12 gram in the extensions. Transpiration of the root-pruned plants was 39.2 per cent less than that of the controls.

Ten days later, July 8, the root-pruned plants were 16 per cent less in average height than the controls. The dry weight of tops was 27.4 per cent less, the number of tillers was reduced 29.7 per cent, and the leaf area 20.8 per cent. The roots in the containers were 1.6 per cent less in dry weight, and those in the extensions 33.3 per cent less. Plants root-pruned but once (ten days previously) had their transpiration losses reduced 40.5 per cent (table I). Transpiration of plants root-pruned for the second time on July 8

TABLE I. *Average per cent reduction in growth and transpiration losses per container of 15 plants at the several periods after the root-prunings*

Criteria	10 days after first root-pruning	10 days after second root-pruning	10 days after third root-pruning
Average height, in.	16.0	31.4	27.5
Dry wt. tops, gm.	27.4	43.3	55.9
Average number tillers	29.7	33.5	6.0
Average leaf area, sq. in.	20.8	24.4	26.0
Dry wt. roots in containers, gm.	1.6	40.8	50.5
Dry wt. roots in extensions, gm.	33.3	30.3	47.5
Dry wt. total roots, gm.	13.6	36.4	49.1
Transpiration, gm.	40.5	42.2	38.0

was reduced 48.7 per cent. Two of the six controls, whose roots were pruned for the first time on this date, had their transpiration reduced only 30.3 per cent, since their root development in the containers exceeded that of plants root-pruned 10 days earlier.

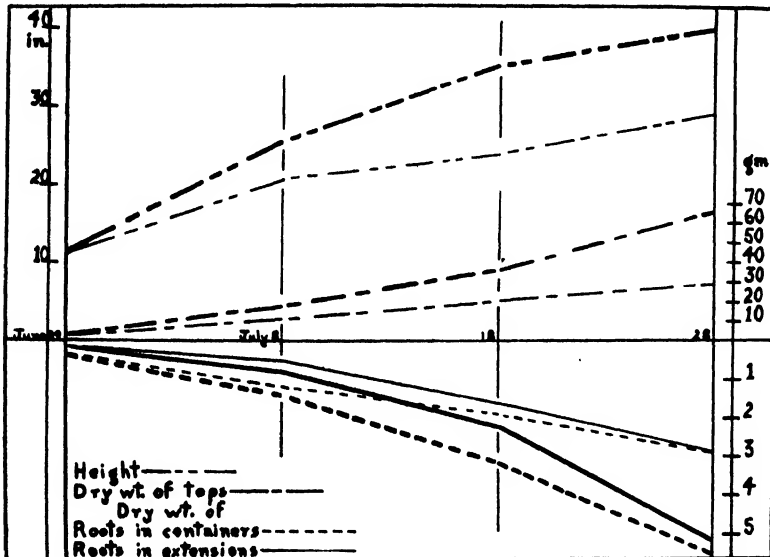


FIG. 1. Relative growth of tops and roots of Sudan grass root-pruned at 5-inches depth (light lines) and controls (heavy lines).

The results for July 18 and 28 are summarized in table I and figure 1. On July 28 the plants were 46 days old and some had been root-pruned three times. The height of the root-pruned plants averaged 27.5 per cent less than the controls. The dry weight of the tops was 55.9 per cent less, the number of tillers was reduced 6 per cent, the leaf area 26 per cent, and the dry weight of roots 49.1 per cent. Plants root-pruned three times, the last time being ten days previously, had their water losses reduced 38 per cent, and the controls, root-pruned for the first time, had it reduced 49.6 per cent. This greater reduction resulted, probably, from the fact that the controls were depending more than were the frequently clipped plants upon the moisture in the deeper soil. Plants root-pruned for the fourth time had their water losses reduced 83.1 per cent.

In the 5-inch containers without extensions, clipping the tops to a height of 4 inches 3 times resulted in a reduction of 85.2 per cent in the dry weight of the roots, compared to the controls with extensions. Plants with neither roots nor tops pruned or clipped gave a reduction of 58 per cent. This was due to the shallow soil. It was approximately as great a decrease as that of plants root-pruned at 5 inches depth. The dry weight of tops of plants clipped at 4 inches, where roots were undisturbed, gave a decrease of 86.2 per cent, and those entirely undisturbed, a decrease of 54.9 per cent. The average number of tillers was reduced 35.3 per cent in the first case and 58.1 per cent in the second.

In the 10-inch series roots were first pruned on July 2, when the plants were 16 inches tall. The average dry weight of the tops per container was 5.89 grams, number of tillers 2.2, and leaf area 17.8 sq. in. The average dry weight of the roots per container was 0.625 gram, and in the extensions 0.13 gram. Transpiration of the root-pruned plants was reduced 20.5 per cent.

TABLE II. *Average per cent reduction in growth and transpiration losses per container of 15 plants at the several periods after the root-prunings*

Criteria	10 days after first root-pruning	10 days after second root-pruning	10 days after third root-pruning
Average height, in.	11.5	17.6	20.5
Dry wt. tops, gm.	9.6	20.7	33.8
Average number tillers	10.8	19.4	14.0
Average leaf area, sq. in.	12.5	14.2	20.3
Dry wt. roots in containers, gm.	4.8	2.5	43.0
Dry wt. roots in extensions, gm.	3.2	19.5	23.9
Dry wt. total roots, gm.	4.4	7.7	36.9
Transpiration, gm.	19.9	27.7	11.9

The results for July 12 and 22 and August 1 are summarized in table II and figure 2. On August 1 the plants were 49 days old and some had been root-pruned three times previously at ten-day intervals. The average height of the root-pruned plants had been reduced 20.5 per cent as compared

with the controls. The dry weight of the tops was 33.8 per cent less, the number of tillers 14.0 per cent, the leaf area 20.3 per cent, and the dry weight of roots 36.9 per cent less. Plants root-pruned three times, the last time only ten days previously, had their water loss reduced 11.9 per cent. The controls root-pruned for the first time had it reduced 13.2 per cent. Plants root-pruned for the fourth time had their transpiration decreased 33.3 per cent.

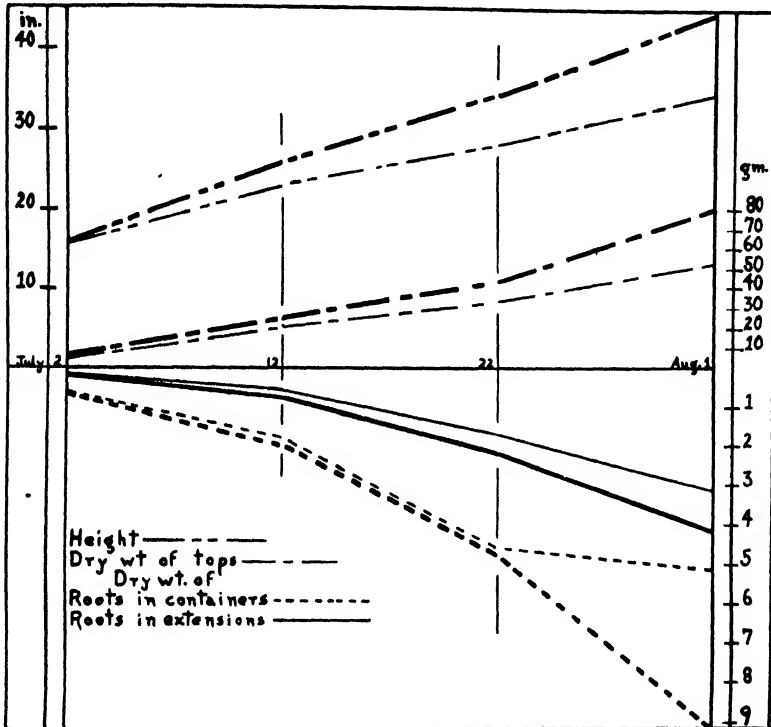


FIG. 2. Relative growth of tops and roots of Sudan grass root-pruned at 10-inches depth (light lines) and controls (heavy lines).

Plants clipped three times to a height of 4 inches in the containers without extensions, gave an average total root production of 1.71 grams per container, which was 87.2 per cent less than the controls. Unclipped and unpruned plants confined to 10 inches of soil showed a 45.9 per cent decrease in dry weight of roots. This was a 9 per cent greater decrease than for plants root-pruned at 10 inches depth. The growth of tops of clipped plants was reduced 80.3 per cent by dry weight, and that of the unclipped ones 42.4 per cent. The average number of tillers was reduced 57.8 per cent in the unclipped and 32.5 per cent in the clipped plants.

Discussion

Roots in the containers continued growth after pruning at 5 inches depth, and new roots developed in the extensions after the old ones were removed. The amount of dry weight, however, was greatly reduced. The reduction in the containers was slight (1.6 per cent) on July 8, but 50.5 per cent by July 28. Likewise in the extensions it increased from 33.3 per cent to 47.5 per cent.² The dry weight of the total root system showed a decrease of 13.6 per cent on July 8 (ten days after the first root-pruning) and 49.1 per

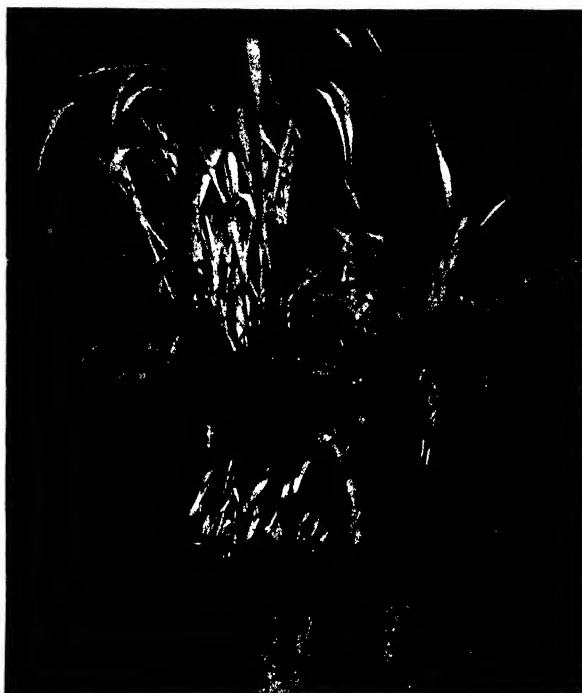


FIG. 3. Sudan grass 40 days old. Plants on the right have been root-pruned three times at a depth of 5 inches; left, controls.

cent by July 28. The dry weight of the tops showed a decrease of 27.4 per cent on the earlier date and a decrease of 55.9 per cent on the later one. The same was true of the leaf area which showed a progressive decrease from 20.8 to 26 per cent.

The roots in the containers and extensions of the 10-inch series likewise showed a decrease when compared to the controls. The dry weight of the total root system had decreased 4.4 per cent for the pruned plants on July 12, and 36.9 per cent by August 1. Decreases in average height, leaf area, and

² Root volumes were also reduced in approximately the same proportion as dry weights in both series, but to conserve space, these data are omitted.

dry weight of tops also occurred. The older the plants the greater were the reductions.

The percentage decrease in every measurement of growth employed was greater in the 5-inch than in the 10-inch series (figs. 3 and 4). An exception was the greater decrease in number of tillers in the 10's at the time of the fourth root-pruning. The cause for this is not clear.

Plants root-pruned at 5 inches depth were unable to produce new roots, either in the containers or extensions, as rapidly as those pruned at 10 inches

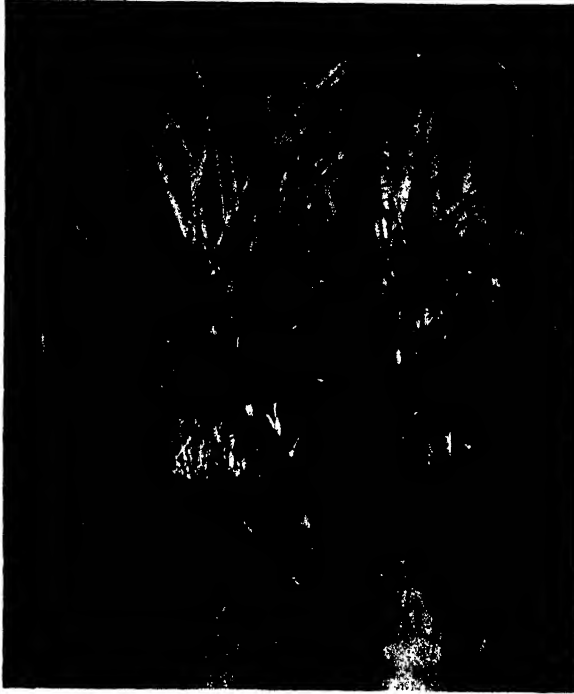


FIG. 4. Sudan grass 40 days old. Plants on the right have been root-pruned three times at a depth of 10 inches; left, controls.

depth. This resulted from the greater growth of the plants in the deeper soil both above and below ground, which in turn was due, no doubt, to the greater volume of soil that supplied more water and nutrients. Moreover, plants in the deeper series were three days older when pruning was begun.

The effect of root-pruning upon transpiration was pronounced. For example, plants root-pruned at 5 inches depth on June 29, gave transpiration losses during that day which were 39.2 per cent less than the controls although the root-pruned plants showed only slight wilting. Eight days later, during which time new root growth occurred, transpiration losses were 34.4 per cent less than those of the controls. Ten days after the root-pruning,

however, the losses were 40.5 per cent less than those of the controls. These differences were due not only to the degree of root reestablishment and increase in growth of tops (and possibly to stomatal closure), but also to differences in the environmental factors promoting transpiration. Similar variable results were obtained throughout the experiment with both series.

In cases where root-pruned plants had a ten-day growth of new roots in the extensions and were not pruned the day transpiration losses were determined, the plants showed greater losses than those that were pruned, but not as great as the controls. The root-pruned plants were the first to wilt on hot, dry days. This resulted from the reduced absorbing surface which for a time deprived them of the water supply in the extensions. Plants in the containers with solid bottoms, and hence confined to 5 or 10 inches of soil, showed reduced transpiration losses as great as 85 and 58 per cent, respectively.

The increase of roots in the containers of the 5-inch series was 597 per cent from the time of the first root-pruning to the end of the experiment, 30 days later. The increase of the controls was 1,310 per cent. Increase of the pruned and unpruned roots in the extensions was 2,175 and 4,233 per cent, respectively. The total root system increased 969 and 1,998 per cent for the pruned and unpruned plants, respectively. In the 10-inch series, the increase of the total root systems of the pruned and unpruned plants during 30 days was 1,017 and 1,671 per cent.

The results reported here are for the summer of 1935. They confirmed in general those of the preceding summer's experiments, which, for lack of space, are not recorded.

Conclusions

Injury of the root system by pruning greatly retarded the development of both roots and tops. Where the roots were pruned at a depth of 5 inches three different times at 10-day intervals, growth was reduced, as measured by dry weight, to about one-half that of the controls. Growth of tops was retarded somewhat more than growth of roots. Similar root-pruning at a depth of 10 inches, but begun when the plants were 3 days older, resulted in an approximate reduction of only one-third in development of tops and slightly more in the production of roots. Thus the deeper the pruning, the less harmful was the effect.

Where roots of undisturbed plants were confined to soil only 5 inches in depth, both tops and roots suffered a reduction of about 55 per cent in dry weight. This was slightly greater than for similar lots of plants that were permitted, during the 10-day intervals between pruning, to absorb from the deeper soil. Clipping of the tops at 4 inches in height resulted in a final reduction of both roots and tops of 85 per cent, where plants were constantly rooted 5 inches deep. Thus periodically removing the tops caused

a greater reduction (85%) in growth of both roots and tops than did a similar pruning of the roots (50%).

Plants rooted in soil 10 inches deep suffered a reduction of 42 to 46 per cent of tops and roots. This was much greater than the approximately 33 per cent reduction occurring in similar plants that extended their roots into the deeper soil during the ten-day intervals between prunings. Clipping the tops at 4 inches in height caused a final reduction in tops and roots of 80 and 87 per cent, respectively. Thus removing the tops caused a greater reduction in growth both above ground and below ground than did a similar pruning of the roots, where the losses were only 33 per cent.

EFFICIENCY OF ABSORPTION BY ROOTS AT DIFFERENT DEPTHS

Relatively few experiments have been performed to determine the efficiency of various portions of the root system in absorbing. During the severe drought of 1934 excellent opportunity was offered to study the activities of plants in absorbing at different depths. Late in June many species of the upland prairies near Lincoln, Nebraska, were wilted and dried due to the exhaustion of available water to a depth of 4 feet (Weaver, Stoddart, and Noll, '35).

Trenching Experiment

A narrow trench 4 feet long was dug to a depth of 32 inches on a hillside in Belmont prairie just above a group of plants selected for study. A second trench, a few feet distant, extended to a depth of 48 inches. Water was poured into the trenches and maintained at a depth of 6 inches during a period of seven days. Water was applied to a similar plot of native vegetation by heavily sprinkling the surface soil.

Results

On the second day after watering, plants in the sprinkled area were noticeably greener. *Antennaria campestris* Rydb. revived quickly and the dominant grass, *Andropogon scoparius* Michx., showed beginnings of greening, which, after another day, were in marked contrast to the surrounding vegetation.

After a week both *Andropogon scoparius* and *Sorghastrum nutans* (L.) Nash had renewed growth for a distance of two feet down the slope from the shallower trench. These species are rooted to a depth of about 4 to 5 feet (Weaver, '19). *Antennaria campestris*, *Poa pratensis* L., and *Panicum scribnerianum* Nash, all species of lesser root extent, made no recovery. Soil sampling at this time showed that water was available only at depths between 2.5 and 4 feet. Near the deeper trench, where available water was to be had only below 3.5 feet, there was no recovery.

Experiments with Cores of Sod

In order to localize the amount of water and control the depth of watering as well as to protect the surface soil from rain, cores of sod were secured during the summer of 1934, and placed in a greenhouse.

Representative sods of thoroughly wilted and dried *Andropogon scoparius*, *Poa pratensis*, *Sorghastrum nutans*, and *Spartina michauxiana* Hitch. were selected with special reference to uniformity of stand. To secure the cores a trench 2 feet wide was dug around a rectangular block of the selected sod. Galvanized iron cylinders, 10 inches in diameter, were then worked down over the cores as they were cut from the earth until the tops of the cylinders were flush with the soil surface. The soil columns were cut off even with the base of the cylinders, which were then fitted with metal bottoms made waterproof by the addition of a paraffin-vaseline mixture. For the first three species the cylinders were 30 inches deep, and each soil core weighed approximately 120 pounds. The roots of *Spartina* were secured to a depth of 48 inches, the soil column weighing about 220 pounds. Three unbroken columns were obtained for each series.

After removal to the greenhouse, the tops were clipped to the soil surface. Cores of soil an inch in diameter were obtained from the center of the columns by means of a Brigg's geotome, the deepest to within 6 inches of the bottom. From these it was ascertained that all water available for growth (*i.e.* moisture above the hygroscopic coefficient of the soil) had been exhausted. Glass tubes three-fourths inch in diameter were inserted to depths of 4, 15, and 24 inches, respectively, in the shorter soil columns and to 12, 27, and 43 inches in the longer ones. Soil was packed tightly around the tubes. These permitted watering at the desired depth in each column. Three liters of water were added to each core. The cores and cylinders were then weighed in order to determine later losses of water by transpiration when the plants renewed growth. Such losses were replaced by watering.

At the end of the experiment each 30-inch core was divided into three equal horizontal sections. The roots were counted, after the cut ends were exposed by washing, at each 10-inch depth. After removing all the soil by continued washing, the dry weight of the roots (exclusive of rhizomes) was determined for each section. The number of stems and dry weight of tops were also ascertained. The 48-inch cores were treated similarly except that they were divided into four equal parts.

Soil samples were taken at the beginning and at the end of the experiment in one soil column, in which plants were growing, watered at a depth of 27 inches. Water content showed a decrease of 0.2 per cent (based on dry weight of the soil) in the first foot, 0.5 per cent in the second foot, and an increase of 4.5 per cent in the third foot. In an extra four-foot core of prairie sod, in which no plants were allowed to grow, water content, taken before and two weeks after adding 3 liters of water at a depth of 12 inches,

showed an increase of 11 per cent in the first foot, 3 per cent in the second foot, and no increase at greater depths. These determinations indicated that, except for absorption, the water remained practically where it was applied, and that differences in the growth of the plants resulted from local absorption of water.

Results

Growth always began earlier where water was applied near the soil surface (table III). The average height of plants and amount of tops were also greatest under this condition (figs. 5 and 6). By far the greatest num-

TABLE III. *Growth of grasses watered at various depths*

Species	Depth watered, in.	First watered	Renewed growth	Ave. ht., in.	Dry wt., gm.	No. stems	Water used, liters
<i>Andropogon scoparius</i>	4	7/12	7/14	8	7.0	124	5.9
	15	7/12	7/15	5	1.8	57	2.5
	24	7/12	7/20	3	0.4	16	1.3
<i>Poa pratensis</i>	4	7/12	7/19	10	5.8	35	4.3
	15	7/12	7/21	8	4.3	45	2.4
	24	7/12	7/25	3	0.4	9	.7
<i>Sorghastrum nutans</i>	4	7/28	7/30	14	6.0	40	4.4
	15	7/28	8/1	7	0.6	11	.8
	24	7/28	8/1	7	0.8	12	1.0
<i>Spartina michauxiana</i>	12	3/15	3/17	42	35.5	16	—
	27	3/15	3/17	39	31.7	13	—
	43	3/15	3/21	25	6.6	8	—

ber and greatest dry weight of roots occurred in the upper 10 or 12 inches of the soil and the least in the lowest layer (table IV). The difference was not so great for *Spartina michauxiana* which has a much deeper root system (often reaching 10 feet) than any of the other grasses used.

TABLE IV. *Average number and yield of roots per container*

Species	Depth, in.	Number	Volume, cc.	Weight, gm.
<i>Andropogon scoparius</i>	0-10	245	69	26.3
	10-20	142	10	3.4
	20-30	82	4	1.3
<i>Poa pratensis</i>	0-10	268	32	13.9
	10-20	145	5	1.7
	20-30	61	2	0.6
<i>Sorghastrum nutans</i>	0-10	156	42	16.6
	10-20	86	8	3.0
	20-30	70	4	1.0
<i>Spartina michauxiana</i>	0-12	95	65	14.3
	12-24	79	25	5.5
	24-36	61	11	1.9
	36-48	44	6	1.0

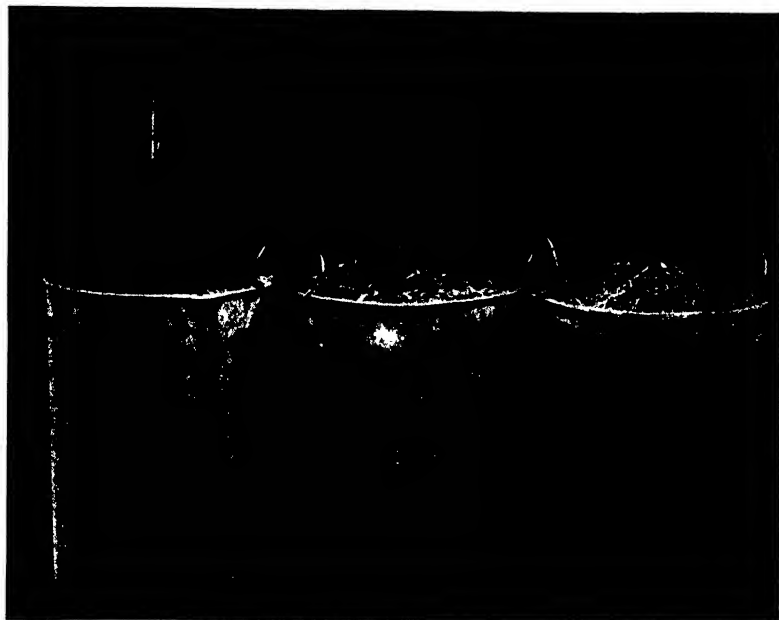


FIG. 5. New growth of *Andropogon scoparius* from June to September, 1934. Watered at depths of 4 inches (left), 15, and 24 inches (right), respectively.

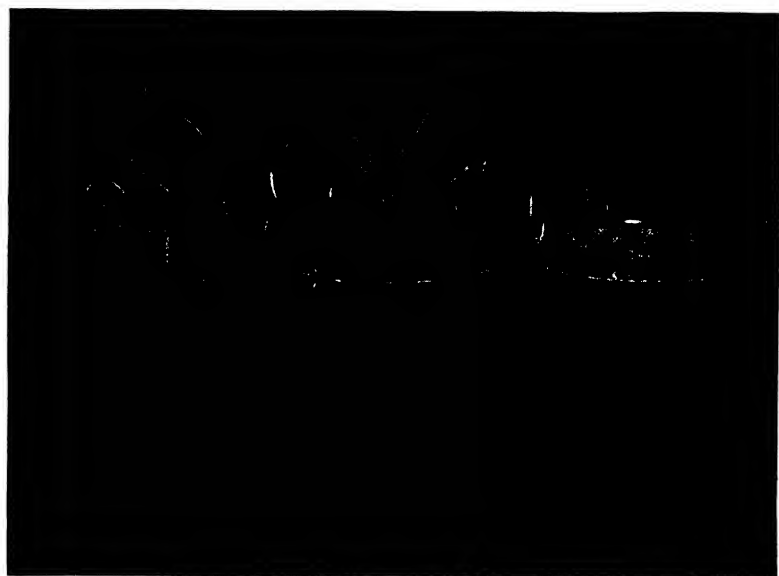


FIG. 6. New growth of *Poa pratensis* from June to September, 1934. Watered at depths of 4 inches (left), 15, and 24 inches (right), respectively.

Andropogon scoparius watered at 4 inches depth produced 4 times as much dry weight of tops as plants watered at 15 inches depth, and 18 times as much as plants watered at 24 inches depth. The upper 10 inches of soil contained 7.74 times as much root material by dry weight as the second 10 inches, and 20 times as much as the third 10 inches. The ratio was 100:13:5.

Poa pratensis produced 1.3 times as much dry weight of tops when watered at 4 inches depth as plants watered at 15 inches, and 14.5 times as much as those watered at 24 inches. The upper 10 inches of soil contained 8.2 times more roots, by dry weight, than the second 10 inches, and 23.2 times more than the third 10 inches. The ratio was 100:12:4.

The behavior of *Sorghastrum nutans* was slightly different. Plants watered at a depth of 4 inches produced 10 times as much dry weight of tops as those watered at 15 inches depth, but only 7.5 times as much as those watered at 24 inches. Dry weight of roots was in the usual sequence. The ratio was 100:18:6.

The deeply rooted *Spartina michauxiana*, watered at 12 inches depth, produced 1.12 times more tops than plants watered at 27 inches depth. Also the shallower watering resulted in the production of 5.38 times as much dry weight of tops as watering at 43 inches depth. There were 2.6 times more roots in the first foot of soil than in the second, 7.4 times more than in the third, and 14.3 times more than in the fourth foot. The ratio was 100:38:14:7.

There was a direct relation between the amount of dry weight produced and the amount of water used. This held even in the case of *Sorghastrum nutans*, where greater top growth resulted from watering at 24 inches depth than at 15 inches. Why this exceptional growth occurred was not determined.

ENCASEMENT OF ROOTS

Native prairie species, all possessing deep taproots, were used in this experiment. Root systems of the mature plants regularly extend to depths of 13 to 20 feet (Weaver, '19). This explains their ability to withstand the frequent droughts of the prairie climate, since the subsoil is always moist (Weaver and Himmel, '31).

The plants were left intact in the field in late autumn and the upper portions of the roots were encased in galvanized iron cylinders 5 inches in diameter. To accomplish this a trench 2 feet wide and 3 to 5 feet deep was dug 6 inches from the plants selected. The roots were then laid bare by removing the soil about them with a hand pick. After the laterals, if any, were cut away, the root was wrapped with gummed fiber tape over a width of several inches near the top and also where it was to hold the lower end of the cylinder. After fitting a cork about the root and inside the end of the cylinder, a warm mixture of 85 per cent paraffin and 15 per cent vaseline was poured in to form a bottom an inch thick when it congealed. The casing was then filled

with dry sand to within an inch of the top, after which it was sealed with an inch of the wax mixture. A double cover of oilcloth was securely fastened around the base of the plant and over the top of the cylinder (fig. 7). The soil was then replaced about the cylinder and the trench filled. Thus the upper part of the root system was enclosed in a waterproof container, while the remainder extended into the moist soil below.

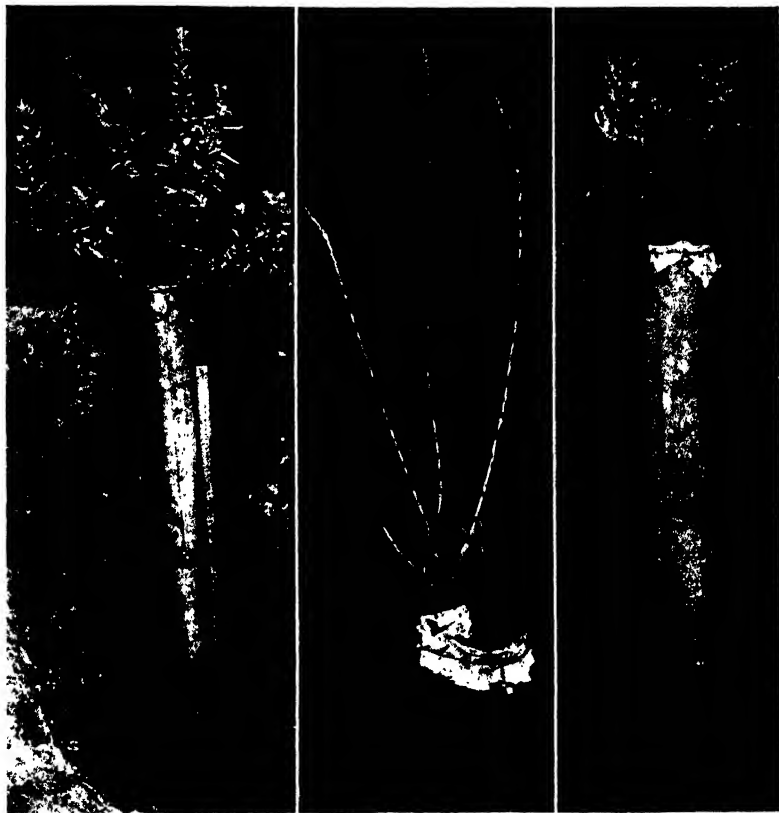


FIG. 7. New growth of *Kuhn timeria glutinosa* (left), *Liatris punctata*, and *Amorpha canescens* (right), after a 10-month interval during which the upper 4 feet of the tap-roots had been encased in dry sand. Photographed Aug. 1, 1935.

Roots of the following plants were thus encased during the autumn of 1934; three false prairie bonesets, *Kuhn timeria glutinosa* Ell., to depths of 3, 4, and 5 feet, respectively; three blazing stars, *Liatris punctata* Hook., to depths of 3, 3, and 4 feet; three rosin weeds, *Silphium laciniatum* L., to depths of 3, 3, and 5 feet; one prairie shoestring, *Amorpha canescens* Pursh, to a depth of 4 feet; and one prairie rose, *Rosa arkansana* S. Wats., to a depth of 3 feet. Fifty-six root systems were excavated to obtain these eleven plants which had roots in a sufficiently favorable position for encasing.

Results

The growth of the plants during the following summer revealed the fact that they were able to absorb sufficient materials from the subsoil to make a vigorous, normal growth. This was similar to neighboring plants of the same species which, because of sufficient rainfall to thoroughly moisten the first four feet of soil, were not deprived of moisture and nutrients in the surface 3 to 5 feet (fig. 7).

Discussion

Alway ('13) has shown that subsoil moisture is drawn upon to a depth of 33 feet by 10-year-old alfalfa plants in northeastern Nebraska. Kiesselbach *et al.* ('29) found that alfalfa in old fields absorbed water at great depths as was shown by irrigating in a trench 10 feet deep. This resulted in much more vigorous growth of the irrigated plants.

Sub-irrigation is not an infrequent natural phenomenon, especially in rugged and mountainous countries. It is frequently indicated by a thriving growth of deeply rooted plants in a climate with very low precipitation. The fact that ground water is capable of maintaining deeply rooted plants such as alfalfa in areas of deficient rainfall is illustrated by agricultural operations in Utah and elsewhere (White, '32).

The results with the forbs are in accord with the findings of Alway, McDole, and Rost ('17) who state that the subsoils of eastern Nebraska are capable of supporting a luxuriant growth of inoculated legumes. Weaver *et al.* ('22) have shown that various crop plants remove both water and nitrates from soil impregnated with this salt to depths of 2.5 to 5 feet. Crist and Weaver ('24) state that roots of crop plants are active in the absorption of both water and nitrate salts even at the maximum depth of their penetration, and that plants receive this supply of water and nitrogen from the deeper soil layers during the latter and perhaps more critical stages of their development.

The abundance of forbs in tall-grass prairie is believed to result largely from the presence of available water at soil levels below those to which most of the grasses penetrate. Among the forbs, resistance to drought was closely correlated with root extent. Species with root systems penetrating deeply into the subsoil were not harmed although for several months little or no water was available in the first four feet.

Conclusions

The dominant prairie grasses employed in these experiments were able to recover, under adverse aerial conditions, from severe wilting and renew growth when water became available at a depth of about 2.5 feet. They were unable to recover when the depth was increased to about 3.5 feet.

Grasses with dead tops renewed growth when the soil was continuously moist at depths of either 4, 15, or 24 inches and, in one species, at 12, 27, and 43 inches depth. The amount of growth decreased rapidly with the depth at which the water was applied, and was closely proportional to the number of roots extending to the several depths.

Deeply rooted forbs were able to produce their normal growth during a season of drought when no available moisture occurred in the first four feet of soil. After the roots were encased so as to prevent absorption to depths of 3 to 5 feet, they continued to develop normally, during a second summer, absorbing only in the deeper subsoil.

SHOOT-ROOT RATIO OF SUDAN GRASS UNDER DIFFERENT DEGREES OF COMPETITION

Sufficient studies have been made on plant competition so that the general significance of the phenomenon has been explained (Kiesselbach, '18; Clements, Weaver, and Hanson, '29; Pavlychenko and Harrington, '34; and others). Peralta's researches ('35) indicated that in early development under severe competition, reduction of roots was nearly proportional to that of tops. Later the roots showed a greater development than the tops in response to the drying soil and the need for increasing supplies of water.

The present study was undertaken to determine the amount of correlation between production of roots and tops under varying degrees of competition for light or water, and for the two combined.

Soil

A plot of Wabash silt loam was selected on low level land near Lincoln, Nebraska. The soil is friable and easily penetrated by roots. The hygroscopic coefficients vary between 10.6 per cent in the first 4 inches and 8.7 per cent in the third foot. The surface layer of soil is acid, pH 4.9, but acidity decreases to pH 5.9 and 6.0 in the second and third foot, respectively.

Methods and Procedure

The plot, 30 by 105 feet in extent, was divided into three equal parts. One part was sown at the normal (N) rate of planting, 22 pounds per acre, the second part at one-third the normal ($\frac{1}{3}$ N) rate, and the third at three times the normal (3 N) rate. Each of these three smaller plots was in turn divided into thirds, in which plants in phytometer cans were grown under competition for both light and water, for water only, and for light only. Each of these nine smaller plots contained 4 cylindrical phytometer cans of sufficient size (up to 10 inches in diameter and 30 inches deep) to permit of normal development of the roots. When filled with field soil of good water content the larger containers weighed 145 pounds. Containers of smaller

size were used in each rate of planting in order to determine the development of the plants at the time when competition began.

In filling the containers, the soil was removed in layers and firmed in the

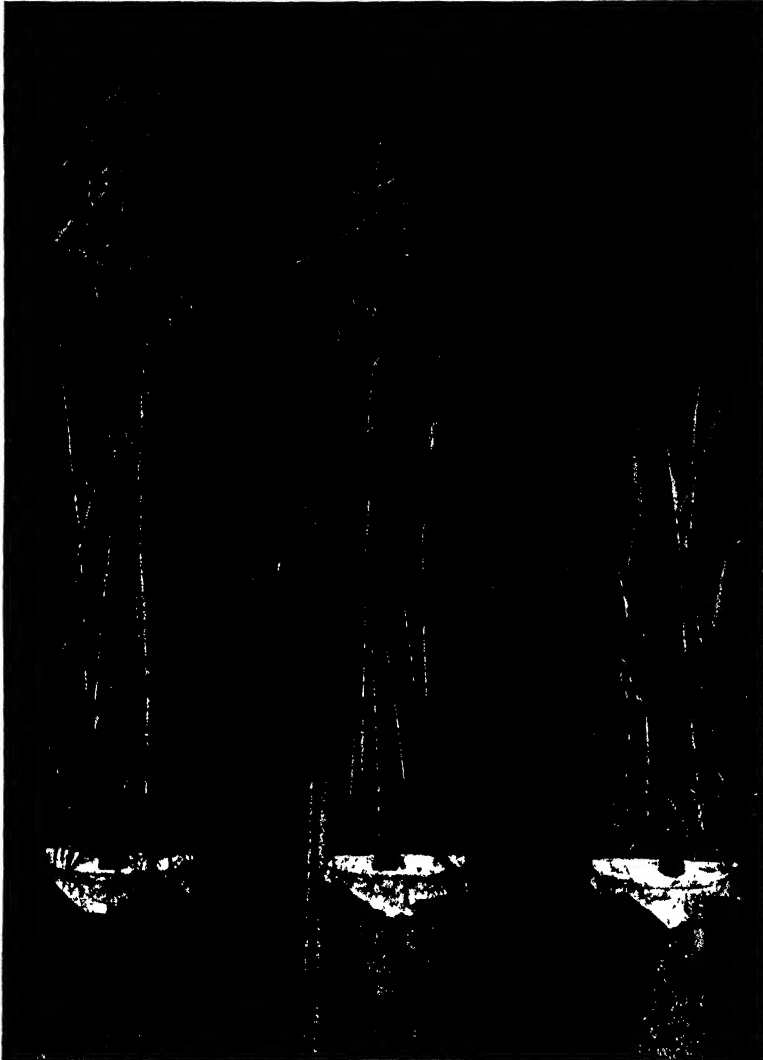


FIG. 8. Sudan grass 45 days old, planted at the normal rate and competing for light only (left), for both light and water (center), and for water only (right).

phytometer cans at depths corresponding to those from which it was taken from the field. The containers in each plot were placed several feet apart and buried so that the tops extended an inch above the soil surface. This

prevented surface water from running in. Each container was covered with an oilcloth top to exclude rain. An opening one-half inch wide and extending the full diameter of the container permitted planting of the seeds and emergence of shoots (fig. 8). A second opening in the oilcloth top, otherwise sealed, permitted watering.

The seeds were sown in the containers on July 8, when seedlings in the field were just appearing, hence all seedlings were later about the same height above the soil. When the plants were 4 inches tall they were thinned to a number which corresponded to the rate of planting in the surrounding field, *i.e.* 2, 6, and 18 seedlings per container in the $\frac{1}{3}$ N, N, and 3 N plots, respectively. At intervals during the course of the experiment, plants competing for light only, in the various rates of planting, were supplied as needed with water totaling 23 pounds per container. This kept the soil well moist at all times. Plants competing for both light and water, and also those competing for water only, were given 7 pounds.

Initial development was ascertained by the examination of the 3 small phytometers, one from each rate of planting, when the seedlings were 13 days old. This was presumed to furnish a basis for the study of future development, but actually competition had already begun. Other determinations were made when the plants were 18, 25, 35, and 45 days old.

The plants surrounding the phytometers competing for water only were cut back when necessary to prevent shading, and the plants in the phytometer cans were separated and tied apart so that all were fully illuminated.

Environmental Factors

Light intensities were measured with a Weston illuminometer at the soil surface in the several rates of planting early in the experiment (July 26). The light was 5, 11, and 23 per cent of full sunshine in the 3 N, N, and $\frac{1}{3}$ N plantings, respectively. Twenty-one days later, in the same sequence, it was 9, 27, and 33 per cent of full sunshine at a height of 3 inches, and at a foot in height 20, 33, and 50 per cent. The light, while often low, was not reduced to the degree desired. This resulted from the dry weather greatly limiting the growth of the plants.

Humidity was determined by means of a cog psychrometer. It was highest in the thicker plantings and lowest in the thinnest, but extreme differences seldom exceeded 10 per cent during the day. The lowest humidities, 35 to 40 per cent, in the several rates of planting occurred where the plants were kept cut back about those competing for water only. Humidities of only 43 to 48 per cent were determined even among the vigorously transpiring plants. This resulted from the light rainfall and intense insolation during this season of drought.

Water content of the soil in the containers of the N plantings was greatest on August 4 (24%), where competition was for light only and least

(18%) where it was for water only. On August 24, the same condition of low water content existed under all three rates of planting. For example in the 3 N, where competition was for light only, the water content was 20 per cent and where it was for water only it was 14.8 per cent. Water content in the various rates of planting and under the same competitive conditions was, however, approximately the same.

Relative Rate of Growth

When the plants were 13 days old, on July 23, the average dry weight of the tops per plant was greatest in the N (0.291 gm.), intermediate in the 3 N (0.204 gm.), and least in the $\frac{1}{3}$ N plantings (0.127 gm.). This is in accordance with the fact that under full insolation and low humidity seedlings thinly spaced frequently develop more poorly than those more thickly grouped. Conversely, where too thickly planted, growth is retarded. The average dry weight of the roots was 0.053, 0.052, and 0.036 grams in the N, 3 N, and $\frac{1}{3}$ N, respectively. Thus as shown by the development of roots and tops, competition had already begun.

Development in Different Rates of Planting

Where competition was for both light and water the dry weight of tops was greatest at first (July 28) in the N planting, intermediate in the $\frac{1}{3}$ N, and least in the 3 N. But by August 4, the thinnest plantings had the greatest dry weight of tops and the thickest were most retarded. The dry weight of roots of the $\frac{1}{3}$ N plants was greatest at the first examination and the 3 N least, a condition that was maintained throughout (table V).

TABLE V. *Average dry weight of tops and roots in grams*

Rate of planting	July 28		August 4		August 14		August 24	
	Tops	Roots	Tops	Roots	Tops	Roots	Tops	Roots
Competition for light and water								
3 N	0.49	0.11	1.08	0.21	1.15	0.22	1.63	0.23
N	0.75	0.14	2.58	0.44	3.16	0.70	4.82	0.94
$\frac{1}{3}$ N	0.66	0.15	3.07	0.51	8.40	1.62	11.45	2.06
Competition for water only								
3 N	0.38	0.11	0.88	0.27	1.10	0.31	1.71	0.53
N	0.60	0.24	2.60	0.70	2.88	0.98	5.35	1.46
$\frac{1}{3}$ N	0.85	0.09	5.39	0.93	9.07	2.27	17.62	4.01
Competition for light only								
3 N	0.40	0.10	0.92	0.12	1.81	0.34	2.84	0.61
N	0.59	0.11	2.80	0.42	4.93	0.96	6.93	1.45
$\frac{1}{3}$ N	0.27	0.03	3.67	0.30	10.58	1.63	21.52	5.06

Where competition was for water only, dry weight of tops on July 28 and thereafter was greatest for the $\frac{1}{3}$ N and smallest for the 3 N. The dry

weight of roots followed the same sequence, except that in early development the dry weight was greatest in the N and least in the $\frac{1}{3}$ N.

Where plants were competing for light only, the N plantings at first were greatest in dry weight of both tops and roots. But the final outcome, as under previous conditions of competition, was that the thinnest plantings exceeded in dry weight of both tops and roots and the thickest plantings were most suppressed (table V).

Among the several rates of planting, the greatest production of tops (21.5 gm.) was in the $\frac{1}{3}$ N where competition was for light only, and the smallest (1.6 gm.) in the 3 N under competition for both light and water. The production of roots was in exactly the same sequence (5.1 and 0.23 gm.) under the same types of competition.

Development in the Same Rate of Planting

Among the N plantings, at the end of the experiment, the greatest dry weight of tops (6.9 gm.) was produced where competition was for light only; intermediate (5.3 gm.) where it was for water only; and least (4.8 gm.) where it was for both light and water (fig. 8). Dry weight of roots, in the same sequence, was 1.5, 1.5, and 0.9 grams.

Among the $\frac{1}{3}$ N plantings, at the termination of the experiment, the greatest dry weight of tops (21.5 gm.) was also produced where competition was for light only; intermediate (17.6 gm.) where it was for water only; and least (11.5 gm.) where it was for light and water. Likewise, weight of roots in the same sequence was 5.1, 4.0, and 2.1 grams.

An exactly similar sequence was found among the 3 N plantings. Dry weight of tops was 2.8, 1.7, and 1.6 grams, respectively, and dry weight of roots 0.61, 0.53, and 0.23 grams.

Ratio of Shoots to Roots

Relative development of roots was greatest where the soil was driest. The shoot-root ratio was least on July 28, under the various rates of planting, where competition was for water only, except for the $\frac{1}{3}$ N planting. In phytometers examined on August 4, 14, and 24 it was still least where competition was for water only, except for the $\frac{1}{3}$ N on the last date. Here it was nearly the same, *i.e.* 4.4:1 and 4.3:1, where competition was for water only and for light only, respectively. Of 36 determinations the shoot-root ratio was least, with 2 exceptions, where competition was for water only, and greatest, with 4 exceptions, where it was for light only.

Discussion

As regards total percentages of increase, the tops and roots increased most in the $\frac{1}{3}$ N conditions and least in the 3 N. For example, the sums of the percentage of increase from one examination to the next were 1,265, 536,

and 299 per cent for tops, and 1,304, 633, and 343 per cent for roots in the $\frac{1}{3}$ N, N, and 3 N plantings, respectively, where competition was for water only. These figures show that roots increased more than the tops under competition for water. In the other competitive conditions, however, the percentages were greatest for tops. Thus where competition was for both light and water, the total of the percentages of increase were 994, 477, and 309 per cent for tops, and 801, 472, and 212 per cent for roots in the $\frac{1}{3}$ N, N, and 3 N plantings, respectively. The greater increase of roots where competition was for water only, resulted from the drier soil in this condition. These findings are confirmed by Peralta ('35) who states that roots in thicker plantings of Sudan grass suffered smaller decreases than did the tops. Haasis ('21), and Crist and Stout ('29) also observed that the greater the available moisture the greater is the shoot-root ratio.

At the close of the experiment, production of roots in N sowings was nearly the same (1.46 and 1.45 grams) for plants competing for water only and for light only, respectively. Otherwise plants competing for light only produced the greatest average dry weight of tops and roots in all rates of planting. Those competing for water only ranked intermediate, and those competing for both factors did poorest (table V). From these results it may be seen that water was the greatest limiting factor.

In competition for both light and water, the ratio of the tops was 100:42:14 and of the roots 100:45:11 in the $\frac{1}{3}$ N, N, and 3 N plantings, respectively. Where competition was for water only, the ratios in the same sequence were 100:30:10 for tops and 100:36:13 for roots. Where competition was for light only similar ratios were obtained. For the tops the ratio was 100:32:13 and for the roots 100:29:12. Thus the average plant production in all cases was far greater in the $\frac{1}{3}$ N, intermediate in the N, and least in the 3 N. This was due to the greater quantity of water available in the thinner plantings. This was true whether water as a factor was acting alone or in conjunction with light, or light alone was the only factor for which the plants were competing. This emphasizes again the fact that water was the more important factor.

Although plants competing for both light and water had an amount of water equal to that of plants competing for water only, repeated soil sampling showed that they did not use as much water as did the plants where competition was for water only. This was due to insufficient light which limited the development of the plants, and both absorbing and transpiring surfaces were smaller than those of plants competing for water only.

Conclusions

Low water content of soil greatly increased production of roots in proportion to the development of the shoots where light was not a limiting factor to growth. The greater the demand for water, with increased thickness

of planting, the greater was the production of roots in proportion to tops. Competition for both water and light also increased root production compared to that of tops, but not to the extent where the fully lighted tops were exposed to greater transpiration losses. Where soil moisture was plentiful and competition was primarily for light, root production was decreased only in proportion as the tops were reduced in size by thicker planting.

The smallest total production of both roots and tops occurred, under all rates of planting, where competition was for both light and water. Conversely, the greatest total production, under conditions of the experiment, occurred where water was abundant and competition was for light only. Thus water content of soil was the master factor in determining not only the yield but also the proportion of roots to tops.

SUMMARY

Roots of Sudan grass were pruned at depths of 5 or 10 inches every 10 days. Between prunings they were allowed to extend into deeper soil. Unpruned plants were maintained as controls. Water losses were restored daily.

Root-pruning three successive times at 5 inches depth reduced the dry weight of tops 56 per cent and that of roots 49 per cent. Roots in the first 5 inches of soil were reduced 51 per cent in dry weight, those at greater depths 48 per cent.

Root-pruning three successive times at 10 inches depth decreased the dry weight of tops 34 per cent and that of roots 37 per cent. Roots in the first 10 inches of soil were 43 per cent less and those at greater depths 24 per cent less than the controls. Thus the deeper the root pruning the less harmful was the effect.

Plants confined to 5 or 10 inches depth of soil were clipped every 10 days at a height of 4 inches; others were uninjured. Plants in soil 17 and 22 inches deep, respectively, were used as controls. Water losses were restored daily.

Dry weight of tops of uninjured plants in 5-inches depth of soil was 55 per cent less than the controls, and dry weight of roots 58 per cent less.

Periodically removing the tops at 4 inches in height caused an 85 to 86 per cent reduction in growth of both roots and tops; pruning of the roots at 5-inches depth resulted in a 50 per cent decrease.

Dry weight of tops of uninjured plants in the 10-inch depth of soil was 42 per cent less than the controls, and dry weight of roots 46 per cent less.

Clipping the tops at 4-inches height caused a reduction of 80 per cent in tops and 87 per cent in roots. Pruning the roots at 10 inches depth reduced both roots and tops about one-third.

Root-pruning resulted in 83 per cent reduction in transpiration of the shallowest rooted plants root-pruned 4 times, and 50 per cent for deeply rooted ones pruned for the first time at 5 inches depth. Among those rooted

10 inches deep and similarly treated, water loss was reduced only 33 and 13 per cent, respectively.

When water had become nonavailable in upland prairie to 4 feet in depth and the plants had dried, large cores of soil 30 to 48 inches deep were secured. These contained nearly pure growths of various prairie grasses. Watering at depths of 4, 15, 24, and 43 inches resulted in new growth of tops.

Growth began earliest and number and dry weight of shoots were greatest in those cores where water was applied nearest the soil surface. Development was delayed in direct proportion to the depth of watering. The largest number and greatest dry weight of roots occurred in the top 10 or 12 inches of soil, and the roots decreased progressively with depth.

Very deeply rooted prairie forbs developed normally even after available soil moisture occurred only below 4 feet. The upper 3 to 5 feet of taproots were excavated and encased in waterproof cylinders in the fall without disturbing the deeper roots. Growth the following summer was equal to that of undisturbed plants.

Sudan grass was grown under three rates of planting to study the relative development of roots and shoots where competition was for water, water and light, and light only.

Soil in large containers, sunk until the tops were even with the soil surface, was planted at the normal (N), $\frac{1}{3}$ N, and 3 N rates, as were also the plots surrounding the containers. Competing field plants greatly reduced the light. They were kept clipped where competition was for water only.

Greatest production per plant of both tops (6.9 gm.) and roots (1.5 gm. in the N plantings) occurred under all rates of planting where competition was for light only. The least (4.8 and 0.9 gm.) occurred where it was for both light and water.

Greatest production of roots in relation to shoots occurred where competition was for water, and the soil consequently the driest. The shoot-root ratio in the N planting was 3.7/1.

Fewest roots were produced in proportion to tops where competition was for light only and the soil was continuously the most moist. The shoot-root ratio in the N planting was 4.8/1.

The final ratios of shoots to roots decreased as the density of planting increased where competition was for water only. They were 4.4/1, 37/1, and 3.3/1, respectively.

Where the soil was favorably moist and competition was for light only, the ratios were higher but no consistent increase or decrease was ascertained.

Water content of soil was the master factor in determining not only the yield but also the proportion of roots to tops.

The author wishes to express his sincere gratitude to Dr. J. E. Weaver for outlining the problem and for direction and encouragement throughout the investigation.

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FOOD HABITS OF IOWA RED FOXES DURING A DROUGHT SUMMER ¹

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The most severe drought which Iowa has suffered in recent years occurred during the spring and summer of 1934. Aside from areas of local precipitation, the drought was not broken until early June in roughly the northern half of the state and not until fall over much of the southern part. Since 1932, the State College in cooperation with the Fish and Game Commission had been carrying on field studies of certain animal populations, and the resulting data give us a fair basis for appraising some of the effects of the drought emergency.

The food habits data from red fox (*Vulpes fulva*) studies may be looked upon as being of particular interest during this period of crisis, insofar as they reflect changes in relative availability of prey types, which seem in turn influenced by habitat changes attributable to the drought. We have for comparison data on spring and summer fox food habits for the "normal" season of 1933 as well as for the drought season of 1934.

The 1933 data have been published, together with a critical description of the chief research techniques used (Errington, '35b); the data for 1934 are herein presented.

As the drought was at its height during the time that the foxes had pups in dens, the collection of food items and fecal samples from such places provided a comparatively simple means of securing contemporaneous data on a large scale. Den studies and fecal analyses have technical drawbacks and should be interpreted and correlated with caution; however, they are well adapted for spring and summer studies, although stomach analyses are in important ways more suitable for use at other times of the year and more reliable for general food habits work.

DEN STUDIES, 1934

The principal criticism to be made against the recording of prey or food items from dens is that the larger carcasses, being more conspicuous and less likely to be eaten entire, are much more likely to be listed out of proportion to the frequency with which they may be brought in.

¹ Journal Paper No. J349 of the Iowa Agricultural Experiment Station. Project No. 330.

It should be stated also that, whereas in 1933 it was the policy of the deputy game wardens (who gathered most of the material) to save very nearly everything found at dens, except rabbits, for the purpose of having counts and identifications checked, the wardens in 1934 merely took notes in the field. We have no way of ascertaining how much this simplified procedure increased the number of items miscounted or misidentified; in some individual instances, considerable error doubtless crept in; on the whole, however, it is probable that the wardens' reports are of fair quality, especially as the majority of the men specifically encouraged to cooperate had demonstrated their reliability the previous year.

Counts of food items were made at 200 fox dens during the season of 1934, and from which 2,848 items were recorded.

Domestic animals or poultry were represented by 438 items (15.38 per cent of the total): goat, 2; lamb, 14; small pig, 40; house cat, 1; pigeon, 2; guinea hen, 3; turkey, 3; chicken, 367; barnyard duck (plus probably some of those listed later among the wild ducks), 2; geese, 4.

Wild mammals totalled 1,404 (49.29 per cent): cottontail (*Sylvilagus floridanus*) and unspecified "rabbit," probably mainly cottontail, 727 (some wardens did not count individuals at dens); jack rabbit (*Lepus townsendii campanius*), 129; Norway rat (*Rattus norvegicus*), 9; muskrat (*Ondatra zibethica*), 38; mice (mostly *Peromyscus* with fewer *Microtus* and *Reithrodontomys*), 220; pocket gopher (*Geomys bursarius*), 96 (possibly including a few ground squirrels listed as "gophers"); fox squirrel (*Sciurus niger rufiventer*), 15; ground squirrels (probably somewhat more *Citellus tridecemlineatus* than *C. franklini*), 124; woodchuck (*Marmota monax*), 8; unspecified skunks, 3; mink (*Mustela vison*), 1; weasels (probably *M. longicauda* for the most part), 14; short-tailed shrew (*Blarina brevicauda*), 2 (probably more were misidentified as "mice"); mole (*Scalopus aquaticus*), 16; opossum (*Didelphis virginiana*), 2.

Wild birds totalled 999 (35.08 per cent): small birds (mostly native sparrows and other Fringillidae), 34; meadowlark (*Sturnella*) and other Icteridae, 81; Turdidae (mostly robin, *Turdus migratorius*), 16; crow (*Corvus brachyrhynchos*), 4; bluejay (*Cyanocitta cristata*), 2; Picidae (mostly flicker, *Colaptes auratus*, and red-headed woodpecker, *Melanerpes erythrocephalus*), 9; unspecified owls, 3; coot (*Fulica americana*), 3; ring-necked pheasant (*Phasianus colchicus torquatus*), 745; bob-white (*Colinus virginianus*), 25; Hungarian partridge (*Perdix perdix*), 59; prairie chicken (*Tympanuchus cupido americanus*), 1; ducks (blue-winged teal, *Querquedula discors*, and mallard, *Anas platyrhynchos*, including some of the latter which were doubtless barnyard ducks), 17.

Only 7 reptiles and amphibians were noted (0.25 per cent): snakes (mostly *Thamnophis* with at least one *Pituophis*), 5; frog (*Rana*), 2.

Reports were made by wardens on 63 additional dens, for which no detailed counts of items were attempted. Some of the items of interest in-

cluded two house cats, a killdeer (*Oxyechus vociferus*), and two ruffed grouse (*Bonasa umbellus*), the latter from the extreme northeast corner of the state.

FECAL STUDIES, 1934

A total of 935 fecal samples were obtained from the vicinity of 32 of the dens observed. The samples were analyzed by myself, with the exception of 207 samples handled by Mr. Kenneth Krumm. Although we had the use of a rather adequate reference collection and received assistance on baffling items from the U. S. Biological Survey, work of this sort is difficult and subject to a certain error under the best of conditions, particularly when badly frayed feathers or crushed and almost digested bone fragments defy further identification.

Of the 935 samples for the spring and summer of 1934, 894 contained recognized mammalian remains: sheep in 1; small pig in 12; cottontail, 367; jack rabbit, 37; undetermined Leporidae, mostly young and probably cottontail, 214; jumping mouse (*Zapus hudsonius*), 3; *Microtus*, 244; *Peromyscus*, 158; *Reithrodontomys*, 4; undetermined mice, 37; pocket gopher, 46; fox squirrel, 1; chipmunk (*Tamias*), 6; *Citellus franklini*, 16; *C. tridecemlineatus*, 18; undetermined ground squirrel, 9; young woodchuck, 5; undetermined Sciuridae, 1; undetermined rodent, 1; striped skunk (*Mephitis*), 1; undetermined skunk, 1; short-tailed shrew, 3; mole, 6; very immature undetermined mammal, 4.

Three hundred four samples contained food debris of recognized avian origin: Fringillidae (native sparrows except for a towhee, *Pipilo erythrophthalmus*), in 22; grackle (*Quiscalus quiscula*), 2; red-winged blackbird (*Agelaius phoeniceus*), 1; meadowlark, 19; shrike (*Lanius ludovicianus migrans*), 1; crow, 2; barn swallow (*Hirundo erythrogaster*), 1; horned lark (*Otocoris alpestris*), 3; flicker, 1; mourning dove (*Zenaidura macroura*), 1; Virginia rail (*Rallus limicola*), 1; domestic chicken, 44; ring-necked pheasant (including young in 4), 107; pheasant egg, 3; bob-white, 1; Hungarian partridge, 18; undetermined gallinaceous birds, 19; mallard, including some possibly from tame ducks, 5; blue-winged teal, 6; undetermined duck, 1; grebe, 1; undetermined birds, 137.

Nineteen samples contained snake, and one fish scales.

Invertebrates recognized were exclusively insects, of which 411 fecal samples contained representations. Most of the insects were Coleoptera of large sizes and were probably caught and eaten by the foxes themselves rather than ingested secondarily as the stomach contents of prey animals.

Insect representations in the fecal samples: *Chrysochus* in 3; *Phyllophaga*, 276; *Geotrupes*, 2; *Canthon*, 4; *Elateridae*, 3; *Necrophorus*, 3; *Harpalus*, 18; *Pasimachus*, 15; *Calosoma*, 21; undetermined Carabidae, 5; undetermined Coleoptera, 81; Diptera, 1; Noctuidae and other Lepidoptera larvae, 68; undetermined insects, 113.

COMPARISON OF THE DATA FOR 1933 AND 1934

A comparison of the fox food habits data for the corresponding seasons of 1933 and 1934 can be conveniently made, as the specimen material was largely gathered by the same men from the same general areas.

As may be readily seen, from checking over the data, few prey species show proportional representation in the carcass debris about dens and in the fecal samples. It seems as if it should be possible to correlate den and fecal representations and to derive some useful coefficients; but this probably could not be done with much satisfaction without experimental data on fecal passage from live foxes fed different types of food. In the absence of data of this sort, we may be able to gain something of an idea of significant changes in fox food habits merely by comparing the percentage figures for the major food items on tables I and II. Considering only those items of fairly fre-

TABLE I. *Comparative representation of food items at fox dens*

Type of prey or food	1933 (113 dens)		1934 (200 dens)	
	Number	Per cent	Number	Per cent
Goat.....			2	0.07
Lamb.....	1	0.1	14	0.49
Small pig.....	19	1.88	40	1.4
Cottontail, and probable.....	284	28.12	727	25.53
Jack rabbit.....	72	7.13	129	4.53
Norway rat.....	1	0.1	9	0.32
Muskrat.....	2	0.2	38	1.33
Mice.....	82	8.12	220	7.72
Pocket gopher, and probable.....	13	1.29	96	3.37
Fox squirrel.....	5	0.5	15	0.53
Ground squirrels.....	33	3.27	124	4.35
Young woodchuck.....	4	0.4	8	0.28
House cat.....			1	0.04
Skunk.....	6	0.59	3	0.11
Mink.....			1	0.04
Weasels.....	5	0.5	14	0.49
Soricidae.....	2	0.2	2	0.07
Mole.....	7	0.69	16	0.56
Opossum.....	1	0.1	2	0.07
Meadowlark.....	10	0.99	55	1.93
Misc. Icteridae.....	5	0.5	26	0.91
Robin.....	5	0.5	15	0.53
Crow.....	8	0.79	4	0.14
Misc. Passerines.....	30	2.97	37	1.3
Picidae.....			9	0.32
Owls.....	2	0.2	3	0.11
Domestic pigeon.....	2	0.2	2	0.07
Mourning dove.....	8	0.79		
Coot.....			3	0.11
Guinea hen.....	2	0.2	3	0.11
Turkey.....			3	0.11
Domestic chicken.....	69	6.83	367	12.9
Ring-necked pheasant.....	314	31.09	745	26.14
Bob-white.....	1	0.1	25	0.88
Hungarian partridge.....	8	0.79	59	2.07
Prairie chicken.....			1	0.04
Tame Anatidae.....	4	0.4	6	0.21
Wild (?) Anatidae.....	4	0.4	17	0.6
American Bittern.....	1	0.1		
Snakes and frogs.....			7	0.24
TOTAL.....	1,010	99.86	2,848	100.02

TABLE II. *Fox fecal samples containing comparable food items*

Type of prey or food in fecal samples	1933 (1,175 samples)		1934 (935 samples)	
	Number contain- ing	Per cent contain- ing	Number contain- ing	Per cent contain- ing
Sheep.....			1	0.11
Small pig.....	6	0.51	12	1.28
Cottontail.....	505	42.98	367	39.25
Jack rabbit.....	26	2.21	37	3.96
Undet. Leporidae, mostly young.....	141	12.0	214	22.89
Norway rat.....	4	0.34	4	0.43
Muskrat.....			6	0.64
Mice.....	762	64.85	446	47.7
Pocket gopher.....	21	1.79	46	4.92
Fox squirrel.....			1	0.11
Ground squirrel.....	56	4.77	50	5.35
Young woodchuck.....	1	0.09	5	0.53
Skunks.....	1	0.09	2	0.21
Soricidae.....	1	0.09	3	0.32
Mole.....	5	0.43	6	0.64
Meadowlark.....	15	1.28	19	2.03
Misc. Icteridae.....	4	0.34	3	0.32
Crow.....	1	0.09	2	0.21
Misc. Passerines.....	34	2.9	27	2.89
Picidae.....	1	0.09	1	0.11
Columbidae.....	1	0.09	1	0.11
Virginia rail.....			1	0.11
Domestic chicken.....	24	2.04	44	4.7
Ring-necked pheasant.....	66	5.62	107	11.44
Bob-white.....	9	0.77	1	0.11
Hungarian partridge.....	1	0.09	18	1.93
Undet. galliformes.....	3	0.26	19	2.03
Anatidae.....	1	0.09	12	1.28
Grebe.....			1	0.11
Undetermined birds.....	253	21.53	137	14.65
Lower vertebrates.....	4	0.34	20	2.14
Insects.....	93	7.91	411	43.96

quent representation in one or both of the seasons of 1933 and 1934, we may note evidence of increased, decreased, or essentially unchanged pressure of foxes upon various prey species.

It should be borne in mind that feces provide a more reliable quantitative index to fox food habits than do most of the items to be seen at dens, and, in the event that feeding trends as shown in tables I and II seem to be contradictory, the data from table II should, as a rule, be given the greater weight.

We may perhaps judge the pressure to have been about the same for 1934 as for 1933 on Norway rats, fox squirrels, weasels and other Mustelidae, Insectivora, and Passerine birds as a whole, including robins, and including Icteridae with the exception of meadowlarks.

Mice were taken to a considerably less extent in 1934, but they constitute such a staple food in ordinary fox diet that a substantial decline in representation would compensate for much greater representation of prey types which are more diffusely utilized.

A slightly greater representation of Leporidae and ground squirrels was indicated for 1934; the same increase of representation would probably hold true for ring-necked pheasants and bob-whites as well, although this is not necessarily the conclusion to be drawn from tables I and II. It is suspected that the 21.53 per cent of undetermined bird representations in table II may contain more pheasant material for 1933 than for 1934.

Most of the 1933 feces containing quail remains were samples from one den, and hence this species was over represented; on the other hand, inadequate samples were received from the 1934 dens about which quantities of quail feathers were distributed, so the lower representation in feces is atypical for this season also.

There appeared to be, in 1934, a heavier proportional representation of lambs and small pigs (including unknown quantities of carrion), meadow-larks, Picidae, and Anatidae. The greatest increase of predation, however, was suffered by muskrats, pocket gophers, domestic chickens, Hungarian partridges, lower vertebrates, and insects.

At the 1933 dens, 537 or 53.17 per cent of the 1,010 items were mammals, and 473 or 46.83 per cent were birds. The 1934 proportions of den items were 1,461 or 51.3 per cent mammals, 1,380 or 48.45 per cent birds, and 7 or 0.25 per cent lower vertebrates.

For 1933, 1,135 or 96.6 per cent of the 1,175 fecal samples were composed almost entirely of mammalian remains; 36 or 3.06 per cent, of avian remains; and only 4 or 0.34 per cent of insect remains. For 1934, 831 or 88.88 per cent of 935 samples were almost entirely of mammalian remains by bulk; 65 or 6.95 per cent of avian remains; and 39 or 4.17 per cent of insect remains.

We haven't the data for exact volumetric computations on the proportions either of species of prey or classes of prey in the 1933 and 1934 fox diets, but we may be justified in making a few generalizations on the basis of work done and field experience. While mammals obviously comprised the principal foods for the two seasons, the representation of this class fell off somewhat in 1934, coincident with a rise in representation of birds and insects.

DISCUSSION

Table III summarizes the data we have on food habits of red foxes in the same general areas for the winters of 1932-33 and 1933-34. While our data for these seasons are too few to give us an adequate basis for comparisons, so far as they go, they do not suggest any significant pre-drought difference in status of staple food items which might explain differences in representation during the spring and summer of 1934.

Population studies of certain wild species, principally in Clay, Palo Alto, and Story Counties, have in some instances given us the means of a better understanding of some of the factors influencing availability of prey species,

not only to foxes but to other predators. Our data on general predation are for the most part unpublished, but they serve very conveniently, for example, in indicating the relative vulnerability or security of a given prey species, notably when other population data on the species may be lacking.

Our trapping and observational data are too limited to be of more than incidental help in evaluating the numerical status and availability of mouse populations to predation. Of our miscellaneous predator data, those pertaining to the food habits of Great Horned Owls (*Bubo virginianus*) and Marsh Hawks (*Circus hudsonius*) are in the best state of organization at present, and the fact that the representation of mice in the diets of both of these species showed a decided increase in the spring and summer of 1934 over that of 1933 indicates that the decreased importance of mice in the diet of foxes was not necessarily due to lower population densities of this type of prey or even to a lowering of availability.

TABLE III. *Comparative representation of fox food items in winter stomachs, intestines, and complete fecal passages*

Type of prey or food representations	1932-33 (29 contents)		1933-34 (50 contents)	
	Number containing	Per cent containing	Number containing	Per cent containing
Sheep (Prob. carrion).....			1	2.0
Cottontail.....	24	82.76	26	52.0
Mice.....	13	44.83	27	54.0
Pocket gopher.....			1	2.0
Ground squirrels.....	2	6.9		
Skunks.....	2	6.9		
Soricidae.....	1	3.45		
Undetermined mammal.....	2	6.9		
Misc. Passerines.....	2	6.9	1	2.0
Domestic chicken (mostly traces).....	7	24.14		
Ring-necked pheasant.....	2	6.9	3	6.0
Bob-white.....			1	2.0
Undetermined bird.....	1	3.45		
Coleoptera.....			1	2.0

The probability seems to be that the availability of mice to foxes may have remained about the same, or possibly may have actually increased, but that the availability of some other prey species may have increased much more proportionally, with the result of deflecting some of the fox pressure from the mice. That the mice did not attain any perceptible relief from general predation is another matter.

Among the species more conspicuously represented in fox diet for 1934, many were obviously more exposed because of cover shortage occasioned not only by the drought directly but indirectly through attendant over-grazing of whatever herbaceous vegetation did grow, along road-sides, fence rows, ditch banks, and in odd corners as well as in pastures.

Muskrats were, of course, placed at a lethal disadvantage in many localities by the drying up of streams and marshes. Concentrations of this species

in some of the remaining potholes were plainly over-populations, and one might expect them to be subject to increased pressure by enemies (Errington, '35c); and where the potholes dried up completely and the animals were evicted to wander about a parched countryside uncongenial even to some terrestrial forms, their increased vulnerability may be taken for granted.

The rise in prominence of the pocket gopher in fox diet is presumably associated with the drought also. It seems most probable that the sparseness of the vegetation during 1934 necessitated increased foraging above ground, which, for these animals, would certainly be attended by an increase of vulnerability.

Meadowlarks, in common with some other ground-frequenting passerine birds, suffered appreciably more from general predation in 1934, so it is not surprising that they were taken in larger numbers by foxes. Nesting conditions for wild ducks were bad in 1934 and were accompanied by greatly increased losses of eggs (Bennett, '35), and it is not beyond reason to postulate that the habitability of the environment for adults may have been likewise reduced.

The apparent increase in vulnerability of Hungarian partridges seems to be associated with rising population densities in local areas. The impression I have gained in the course of recent field studies is that there has been something of a decline in the pheasant population in Northwest Iowa through over-shooting, among other things, and a corresponding rise in the comparatively unshot Hungarian partridge population. Unfortunately, we have few real data on this point.

Pheasants and particularly bob-whites were handicapped during the drought by the shrinkage of habitable environments (Errington, '35a; Hamerstrom, '36), and Hungarian partridges evidently were, too. If a rise in density of the Hungarian partridges had actually occurred, their position would doubtless have been made still more insecure, and this we think may probably have happened.

In the absence of data regarding the proportions of carrion and killed prey among the lamb, pig, and chicken representations, we can hardly arrive at any valid conclusion as to the causes of the rise in importance of barnyard animals in the diets of the foxes. Domestic in common with wild species were affected in various ways by the drought, and it is not inconceivable that their vulnerability to the attacks of predators was correspondingly increased.

The drastically diminished amount and quality of the ground cover provides about the most reasonable explanation for the very evident rise in importance of May beetles as a food item. The entomologists at the Iowa State College, who have been working on *Phyllophaga*, are of the opinion that these insects were not appreciably more abundant in 1934.

The rôle of insect material in the 1934 fox diet is even greater than it appears at first glance. In addition to the 39 fecal samples which were made

up almost entirely of insect remains in 1934, 74 others contained large quantities, and the total amount of insect debris in the season's samples may be estimated at about 10 per cent by bulk. For 1933, the total amount of insect debris in the samples may be estimated at about 1.5 per cent by bulk.

It then appears that, of the miscellaneous food items rising in importance in 1934, the real balance was swinging away from mice toward insects and toward a few vertebrates, notably pocket gophers and domestic chickens.

I seriously question that this swing was in actuality forced by lessened availability of mice or other species taken more often in 1933. At the height of the drought, predators were present in substantial numbers on most of our observational areas and seemed to be having no trouble getting enough to eat, nor did they even seem to approach the limits of their conveniently procurable food supply.

SUMMARY

Comparisons were made of the food habits of red foxes in Iowa during the drought season of 1934 and the "normal" season of 1933. The data were obtained from the examination of 1,010 food items and 1,175 fecal samples from 113 breeding dens in 1933 and 2,848 food items and 935 fecal samples from 200 dens in 1934.

From this material, the conclusions may be drawn that, of the chief types of food, the representation of rabbits, ground squirrels, passerine birds, and ring-necked pheasants was nearly the same in 1934 as in 1933; that the representation of mice dropped appreciably in 1934, coincident with a rise in representation of pocket gophers, domestic chickens, and insects (mainly such Colcoptera as *Phyllophaga*).

The increase in representation of insects in fox diet was especially pronounced.

On the basis of contemporaneous data from population studies of certain prey species and studies of the food habits of predators other than foxes, it would appear that the adverse effects of the drought upon the general habitat of prey species was followed by increased vulnerability of most of the latter, only some were rendered more vulnerable than others, and were accordingly preyed upon the more.

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QUANTITATIVE STUDY OF THE ENTIRE ROOT SYSTEMS OF WEED AND CROP PLANTS UNDER FIELD CONDITIONS ¹

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Upon germination the embryonic plant previously dormant in the seed is released. For the first time it comes in contact with the surrounding environment through the medium of its tap or seminal roots. Normally this occurs under the surface. For several days from germination to emergence the young seedling develops rapidly in darkness without any photosynthetic process at work. During all this period the plant's roots are the only observable organs to support new life developing from the seed.

To appreciate fully the significance of roots for the survival of a plant, one must recognize, that during this early embryonic development and before it emerges above the surface, its size is increased from 300 to 400 per cent. This enormously great work must be attributed almost entirely to the activity of the plant's roots.

In a study made recently ² an average root system of Marquis wheat measured at emergence 12.62 inches in a greenhouse and twice that length when grown under field conditions. The corresponding figures for Hannchen barley were 14.75 and 27 inches; for Banner oats 6.6 and 14 inches; for wild oats, *Avena fatua*, 6.95 and 13 inches; for Russian thistle, *Salsola kali*, 1.5 and 2.75 inches, and for wild mustard, *Brassica arvensis*, 2 and 5 inches. Any serious damage to the roots at this time invariably leads to the death of the entire plant.

Thus equipped with organs for absorption of the soil solution, the plants emerge above the surface and start competing with one another as soon as their root systems begin to occupy the same feeding ground (Pavlychenko and Harrington, '35). From that time on until maturity the underground competition continues and its effects are reflected by the corresponding development of the aboveground parts. The extent of the top growth is a direct result of the causes operating underneath the surface.

Root study, therefore, provides a key to a proper interpretation of the aboveground plant development. To be of full value, however, the root sys-

¹ Contribution from the Field Husbandry Department, University of Saskatchewan, Saskatoon, Canada, with financial assistance from the National Research Council of Canada, and in 1935 from the Searle Grain Co. of Winnipeg, Canada. The paper was presented before the annual meeting of the Ecological Society of America at St. Louis, Missouri, December, 1935.

² Unpublished data by the writer.

tems with their smallest branches should be extricated from the ground in their entirety. Their vertical penetration and lateral spread as well as their quantity and distribution at different ground levels must be observed and recorded; otherwise the results are misleading and do not clarify the problem.

PREVIOUS WORK

For the last two centuries strenuous efforts have been made to unveil the underground picture of plant life. Hales (1727) perceived the idea that the quantitative extent of root systems has a profound and direct bearing upon the productive potentialities of plants. His attempt did not result in a definite study on account of his methods being too crude for the task. The efforts, however, were renewed by Nobbe (1862) and at the end of the nineteenth and with the beginning of the present century the problems of root study attracted the attention of broadminded scientists in all fields of plant science.

Due to the fact that the most active young roots, and particularly their branches and root hairs, are extremely fine and fragile and very intimately bound with minute soil particles, their separation from the ground under field conditions offers a task of utmost difficulty. For this reason some investigators have turned their attention to water cultures although they might have realized that results obtained under such highly artificial conditions would have mostly theoretical and indicative values. Many others used potted plants grown in a greenhouse in spite of the data thus secured being very misleading. The majority of workers, however, dealt with plant material grown in the open. Schubart (1855), Hellriegel (1887), Goff (1883), Hays (1888, 1892), King (1893), Schulze ('06), and their followers made vigorous attempts to extricate the entire root systems from the ground. The methods which they use in this work allowed them to separate a good proportion of the main roots from the soil. The strain, however, was too great for the finest roots and these usually were mostly lost. They obtained extremely valuable information, however, regarding the root habits of different plants, but could not secure the tender laterals in sufficient numbers to warrant a quantitative representation of their root systems. After these attempts the idea of the quantitative root study appears to have been abandoned to a great extent. The leading scientists, both in agriculture and plant ecology, worked almost exclusively on root habits by tracing the main roots directly in the ground.

Rotmistrov ('09, '26), Cannon ('11), Weaver ('19, '20, '22) and their followers have investigated hundreds of wild and cultivated plants, and have produced results of classical value. Their work has cleared the way for the comprehensive quantitative study of the entire root systems of economically important plants.

ROOT STUDY AT THE UNIVERSITY OF SASKATCHEWAN

In 1930, the University of Saskatchewan and the National Research Council of Canada undertook jointly the fundamental research on weeds with the object of studying the features responsible for their noxiousness in the cultivated field. During the growing season of 1930 the root systems as well as the tops of the most important weeds and field crops were carefully observed. The observations seemed to indicate definitely that the roots of the pests were primarily responsible for their noxiousness, whereas those of the crops conditioned their success or failure in suppressing the volunteer growth. To confirm these observations it became necessary to obtain quantitative data on the entire root systems of the plants concerned.

Extensive trials over a period of two years eventually resulted in a satisfactory method for the extrication of entire root systems of plants grown under ordinary field conditions. Briefly it consists of: Growing plant material in the open under ordinary field conditions; excavating the plants at desirable stages of their development in sufficiently large blocks of soil to include their entire root systems at each stage; encasing and elevating the blocks to the surface; washing off the earth from the blocks, beginning from the bottom by means of an adjustable nozzle specially constructed for this purpose; charting the root systems on graph paper so that the exact position of the main roots in relation to the surface and the central axis could be clearly defined; preserving the root systems for detailed analyses; analyzing the root systems under water in large tanks specially constructed and illuminated for this purpose; and mounting and photographing of the root systems under water when desirable.

ECOLOGICAL ENVIRONMENT

The experimental plant material was grown in practically flat prairie as found around Saskatoon, Saskatchewan, in a dark brown, light loam of the Plains-Park transitional zone. The profile is dark, soft and cloddy down to about 12 or sometimes to 14 inches in depth. Below this level it becomes lighter in color, contains more sand with occasional grains of coarser gravel. At the depth of approximately 5 feet, a layer of fine sand often occurs. This varies from 6 to 10 inches in thickness and rests on a rather hard bottom of unknown thickness. The air temperature fluctuates between -40° and $+103^{\circ}$ F. and the average annual precipitation is 13.5 inches, most of it coming during the growing season. Winds of high velocity, frequently exceeding 30 miles an hour, prevail particularly during the spring months and accelerate the loss of soil moisture. Dry periods of various durations occur causing crop failures and dormancy of the native vegetation. Long hours of intense sunshine from March to November promote a rapid growth if other conditions are favorable.

Plot Technique and Plant Material

A reasonably uniform half acre block of this land was devoted to the root study. In one section of this area single plants of weeds and crops grew each in the centre of a plot 10 feet square, to eliminate competition of any kind with neighbouring plants. The adjacent area of the same block was sown to various cereals in six inch drills. Between the cereal rows of each plot eight common weeds were sown in strips in such a manner that uninfested cereal checks were provided next to the infested strips.

Six replicates were sown in each case. One of these was used for the excavations planned, while the other five were harvested for top growth determinations at maturity. In this work the usual plot technique was employed, but all records were taken from the date of emergence, which represents a definite stage of plant development.

At 5, 22 and 40 days after emergence and in certain cases at maturity the plants were excavated and their root systems studied. Blocks $14 \times 14 \times 14$ inches were used for 5 day plants; $24 \times 24 \times 32$ inch blocks for 22 day material; $26 \times 26 \times 42$ inch for 40 day and $32 \times 32 \times 66$ inch blocks at maturity. While in the hole each block was properly shaped, encased in a strong wooden frame of proper size, tipped over on its side and elevated to the surface by means of a powerful block and tackle suspended from a strong wooden tripod, 12 feet high. Care was taken to excavate blocks beyond the penetration of the roots at each stage. Washing was done beginning from the bottom end of each block. As the soil was gradually washed away, the tips of the deepest roots appeared one after another and were individually recorded both graphically and by special notes, indicating their exact position in the vertical and horizontal plane and more detailed notes made concerning occasional points of interest. The root systems thus freed from the earth were preserved and analyzed in the winter. The analyses were invariably done in water, and consisted of the following phases: separation of individual root systems from those of their associates; counting and measuring different root structures and estimating their quantitative values; reestablishing their natural positions according to the field charts and notes; and mounting and photographing the specimens while in water. The root systems thus analyzed may be permanently preserved if desirable for demonstration purposes. With this method it was possible to obtain entire root systems of both weeds and cereal crops, in which branches less than one-tenth of a millimeter in diameter and over 128 cm. in length were practically all present with their original root tips. This shows that the quantitative study of entire root systems is not a dream but a real possibility.

Employing this technique, several experiments have been carried on since 1931 each pursuing different phases of the same problem.

QUANTITATIVE STUDY OF ENTIRE ROOT SYSTEMS OF WEED AND CROP PLANTS

It was thought desirable first of all to secure data concerning the plants grown under average field conditions. Strips of wild oats, Marquis wheat, Prolific spring rye, and Hannchen barley were sown in rows 6 inches apart. At 5, 22 and 40 days after emergence and at maturity a number of plants of wild oats and of cereal crops were excavated and their root systems studied. Some data obtained from this work are given in table I.

Each figure in table I is an average from five representative plants. The data for all four stages concerning the same character are grouped together so that their progressive development from emergence to maturity may be traced. Considering the number of seminal roots per plant, wild oats and the three cereals may be placed in order of the increasing values as follows: wild oats 3, Marquis wheat 4.5, Prolific spring rye 5.2, and Hannchen barley 6.6. The detailed analyses of other different characters in the seminal root systems from emergence to maturity reveal the fact that this initial placing is retained by each plant throughout its entire life. At maturity, for instance,

TABLE I. *Quantitative study of the entire root system of weed and crop plants grown in six inch drill rows under ordinary field conditions and excavated at 5, 22 and 40 days after emergence and at maturity, 1934*

Characters studied	No. days after emergence	Wild oats	Marquis wheat	Prolific spring rye	Hannchen barley
Number of seminal roots	5	3.0	4.4	5.4	6.6
	22	3.0	4.6	5.4	6.6
	40	3.0	4.4	4.8	6.6
	80	3.0	4.6	5.2	6.6
Their length less branches	5	13.4	30.4	35.2	57.8
	22	75.4	135.4	147.6	175.0
	40	114.0	139.8	156.2	257.2
	80	132.0	171.2	194.0	283.0
Greatest penetration	5	7.0	8.8	8.0	11.0
	22	24.6	28.8	29.0	28.0
	40	39.6	38.4	39.0	39.0
	80	46.0	45.2	46.0	46.0
Number of branches 1st order	5	35.6	106.6	304.6	391.4
	22	385.8	928.2	1511.2	1582.4
	40	1068.6	1611.4	2215.4	4176.0
	80	1270.0	1873.0	2919.0	4720.0
Their length	5	19.8	36.4	109.2	155.0
	22	1376.4	2152.8	4224.0	5232.8
	40	3176.0	6663.4	4776.0	8798.0
	80	6020.0	8110.0	9100.0	11370.0
Total length of seminal root system	5	33.2	66.8	144.4	212.8
	22	1453.8	2288.2	4371.6	5407.8
	40	3290.0	6803.2	4932.2	9055.2
	80	6152.0	8281.2	9294.0	11653.0

TABLE I. (Continued)

Characters studied	No. days after emergence	Wild oats	Marquis wheat	Prolific spring rye	Hannchen barley
Number of crown roots	5	2.0	0	0	0
	22	7.6	10.6	9.6	11.2
	40	11.8	9.0	11.4	11.2
	80	17.0	11.0	12.2	13.0
Their length less branches	5	1.8	0	0	0
	22	57.8	32.4	54.4	58.6
	40	98.6	37.8	129.4	70.6
	80	318.0	129.0	193.0	231.0
Greatest penetration	5	0	0	0	0
	22	17.0	5.6	12.4	5.8
	40	36.4	5.6	34.2	13.2
	80	46.0	28.0	44.0	31.0
Number of branches, 1st order	5	0	0	0	0
	22	526.4	297.0	1244.0	592.6
	40	1356.0	439.4	2339.6	1348.9
	80	2940.0	912.0	3170.0	3084.0
Their length	5	0	0	0	0
	22	315.6	123.2	690.6	183.6
	40	2848.0	148.4	3060.0	849.2
	80	8839.0	1790.0	3820.0	4080.0
Total length of crown root system	5	1.8	0	0	0
	22	373.4	155.6	745.0	242.0
	40	2946.6	186.2	3189.4	919.8
	80	9157.0	1919.0	3993.0	4311.0
Length of entire root system	5	35.0	66.8	144.4	212.8
	22	1825.2	2443.8	4116.6	5650.0
	40	6236.6	6989.4	8121.6	9975.0
	80	15309.0	10200.2	13287.0	15964.0

the total length of their seminal root systems occupy exactly the same places, *i.e.*, wild oats 6152 inches; Marquis wheat 8281 inches; Prolific spring rye 9294 inches; and Hannchen barley 11,653 inches. This shows that an additional seminal root is of extreme importance to the plant and has a decisive bearing upon what its root system is likely to be at maturity. The significance of this correlation may be fully appreciated only if one is aware of the fact that under dry farming in the years of abnormally low rainfall the cereal crops are supported throughout the growing season exclusively by their seminal root systems, the crown roots remaining undeveloped due to the lack of moisture. An extensive seminal root system at early stages is also important in view of the fact that at this particular period a deciding battle is being fought between the crops and volunteer species for priority in the field toward harvest. One or two additional seminal roots place the plant at a great advantage over its competitors. This is why on land equally infested with wild oats, barley may produce a reasonably clean crop, while wheat fails.

The same table gives quite different results concerning the crown root systems of the same plants. Wild oat produced the crown roots at a much earlier date and in much greater numbers than any of the cereal crops. Due to this fact, at maturity its crown root system had excelled those of wheat, rye and barley by 4.7, 2.3 and 2.1 times respectively. By developing larger numbers of the crown roots the wild oat made up for the deficiency of its seminal root system. According to the total lengths of the entire root systems at maturity, the plants should be placed in order of the increasing values as follows: Marquis wheat, 10,200 inches; Prolific spring rye, 13,287 inches; wild oats, 15,309 inches; and Hannchen barley 15,964 inches.

The results strongly suggest the following deduction. The wild oat is a weak plant in its early growth stages due to the small number of its seminal roots. At this stage it may be successfully suppressed by the uniform stand of cereal crops with more extensive seminal root systems. If the weed survives this period, there is no chance for a crop to smother it after its extensive crown roots are developed.

EFFECT OF COMPETITION UPON DEVELOPMENT OF ROOT SYSTEMS

As the next step, the problem of competition between plants variously spaced was taken up. It was obvious that the plants analyzed in table I did not represent their best possible development. Growing in the six inch rows with 18 to 20 individuals to a foot, they were competing with one another, mutually depressing their normal development. Such a situation generally prevails both in virgin land and under cultivation. Therefore, one nearly always has to deal with plants thus depressed by competition without having any standard measurement for the extent of the reduction thus produced. These considerations lead to an experiment where several single plants of wild oat, Marquis wheat and Prolific spring rye each grew in the centre of an area 10 feet square. This spacing entirely eliminated competition with neighbouring plants. Next to the single plants, strips of wild oats and the two crops were sown in 6 inch drills, with 18 to 20 plants to a foot. The seeding was done at the same time, on the same type of soil, and in the same year. The only difference between the two sets of material was that the single plants received maximum growth conditions, while plants in the 6 inch rows had to compete for them. It was expected, therefore, that the root systems of the single plants would attain their best possible development, which might be considered to be normal under the set of conditions of that particular season. The plants from the 6 inch rows however, would suffer to a certain extent from competition and their root systems would be proportionately reduced. By comparing the resulting root development from the two sets of material it was believed the effects of competition might be demonstrated in a statistical manner.

At maturity both single and 6 inch row plants were excavated and their root systems analyzed. Table II gives the most important data from this experiment. These data are exceedingly interesting yet they are too numerous to be discussed individually. Those interested in the subject will be well advised to study the results in detail as presented in the table. The differences are so great that it suffices to mention only the total length for the entire root systems. The entire root system of the wild oat single plant grown free from competition measured 3,456,005 inches, or 54.3 miles, whereas that of the competing plant measured only 38,452 inches or .6 miles. The ratio between the two is 1:0.011.

TABLE II. *Effect of competition upon the development of root systems under field conditions, 1934*

Characters studied	Wild oats		Marquis wheat		Prolific spring rye	
	Single plant spaced 10 ft. each way	Plant from six inch drills	Single plant spaced 10 ft. each way	Plant from six inch drills	Single plant spaced 10 ft. each way	Plant from six inch drills
No. seminal roots	3	3	5	4.4	5	4.8
Their length less branches	189	132	300	167.0	268	176.0
Greatest penetration	63	48	63	46.0	62	45.6
No. branches, 1st order	1,486	1,164	4,208	1,800.0	4,484	2,517.0
Their length	20,800	3,416	37,900	7,380.0	41,000	8,674.0
No. branches, 2nd order	121,000	27,000	223,000	48,820.0	280,000	5,790.0
Their length	298,000	20,800	312,000	19,840.0	423,000	21,980.0
Branches, 3rd order	Not determined					
Total length of seminal roots	318,989	24,348	350,200	27,387	464,268	30,830
No. crown roots	96	17	73	12.0	168	13.0
Their length less branches	2,016	234	1,021	123.0	2,107	167.0
Greatest penetration	63	46	63	42.0	62	42.0
No. branches, 1st order	23,000	4,213	17,800	1,700.0	21,000	2,619.0
Their length	216,000	6,240	196,000	2,260.0	232,000	4,011.0
No. branches, 2nd order	2,263,000	43,400	1,738,000	14,000.0	2,068,000	10,800.0
Their length	2,859,000	7,630	2,254,000	4,380.0	2,416,000	3,400.0
Total length of crown root system	3,077,016	14,104	2,451,621	6,763	2,650,107	7,578
Total length of entire root system	3,456,005	38,452	2,802,821	34,150	3,114,375	38,408

The corresponding figures for Marquis wheat are 2,802,821 and 34,150 inches respectively and their reduction ratio is 1:0.012; for Prolific spring rye 3,114,375 and 38,408 inches giving a reduction ratio 1:0.012. The results show that due to competition the root systems were reduced from 83 to 99 times in different species. It is interesting to note that the differences between their top developments were equally striking.

It seems that the data just presented give at least some criteria with which to judge the root systems developed under different intensities of competition.

ANALYSIS OF ONE CROWN ROOT SEPARATED FROM THE WILD OAT PLANT

For the purpose of illustrating the method employed in the work presented in table II, one crown root from the wild oat plant therein studied was separated and fully analyzed. The actual root with its branches of various orders is shown in figure 1. The quantitative results are given in table III.

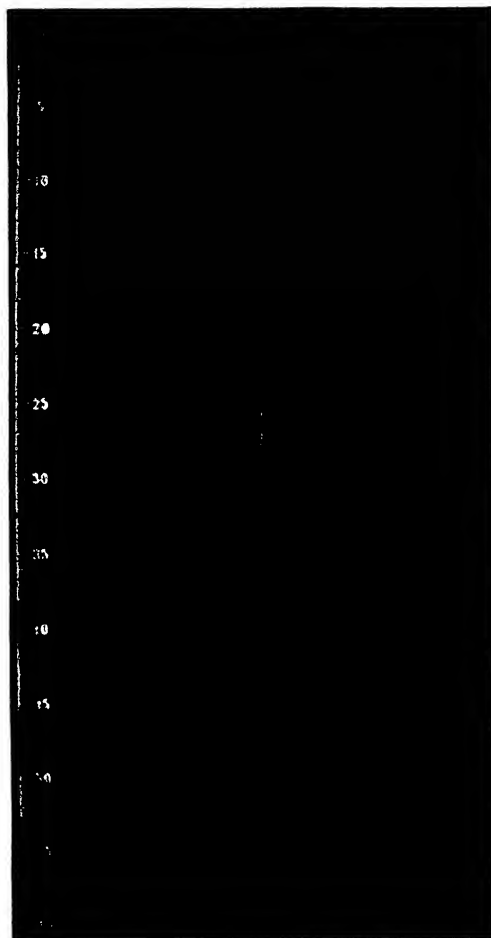


FIG. 1. One crown root of wild oats separated from the root system. The combined length of its branches is 4.5 miles.

As may be seen from table II, column I, there were 96 crown roots to the single wild oat plant. Some of them were comparatively short, but many reached a length of 63 inches. One of these was carefully separated from the plant and studied in all details. The actual counting showed that there were 676 branches of the first order to this root. Only a few of these were

slightly damaged, the bulk being separated in their entirety, each bearing its original root tip. Their frequency on the main root varied within the limits of from 9 to 17 to a linear inch, the largest numbers occurring at the depths from 10 to 15 inches below the surface. Their lengths also varied at different depths, the longest branches being at 10 to 15 inches in depth. At this level many branches were from 43 to 51 inches long, each bearing several hundred

TABLE III. *Detailed study of one crown root separated from the root system of a single wild oat plant grown in the centre of an area ten feet square*

Characters studied	Depth	Data
Length of main root		63 inches
Longest branch of 1st order		51 inches
Frequency of branches of 1st order at	0 to 5 inches	9
	5 to 10 inches	13
	10 to 15 inches	17
	15 to 20 inches	16
	20 to 25 inches	11
	25 to 30 inches	11
	30 to 35 inches	10
	35 to 40 inches	12
	40 to 45 inches	10
	45 to 50 inches	10
	50 to 55 inches	11
	55 to 60 inches	11
Average length of branches of 1st order at	0 to 5 inches	34 inches
	5 to 10 inches	41 inches
	10 to 15 inches	49 inches
	15 to 20 inches	46 inches
	20 to 25 inches	40 inches
	25 to 30 inches	36 inches
	30 to 35 inches	27 inches
	35 to 40 inches	18 inches
	40 to 45 inches	10 inches
	45 to 50 inches	4 inches
	50 to 55 inches	2 inches
	55 to 60 inches	.75
No. branches of 1st order		676*
Their total length		19,675†
Longest branch of second order		13 inches
Average frequency per linear inch		13
Greatest depth at which they occur		48 inches
Their total length per root		237,000 inches
Their total no. per root		145,500 inches
Total length of entire root		256,675 inches
or		4.5 miles

* The branches of 1st order were actually counted and measured.

† The value is a sum of results obtained by multiplying the actual number of branches at each depth by their average length.

of the second order laterals. The total length of the first order branches was 19,675 inches (see footnotes to table III). Down to 48 inches in depth every branch of the 1st order bore laterals of the second order at an average rate of 13 to a linear inch. There were 145,500 of these to the whole root, measuring altogether 237,000 inches. There were also numerous branches

of the 3rd and 4th orders, but not in sufficient numbers to give a reliable basis for their estimation. The total length of this one crown root with the branches of the 1st and 2nd order is 256,675 inches, which equals 4.5 miles. The study shows great possibilities for very detailed quantitative root study, which alone can answer the question: What does the individual root really mean in the plant's life?

EFFECT OF WEED INFESTATION ON THE DEVELOPMENT OF ROOT SYSTEMS OF CEREAL CROPS

Under most conditions the crop plants and volunteer weeds form associations in the cultivated fields. The two groups of plants antagonistic in their economical purpose utilize the limited resources of the land with the result that both are proportionately reduced in their development. For the purpose of determining to what extent the productive resources of the cultivated land are exploited by the roots of crop and weed plants the root systems of plants growing side by side but belonging to the two different groups were studied. In this experiment crops were sown as usual in the 6 inch drills and the common annual weeds between the cereal rows so as to simulate closely ordinary crop fields with average infestation of the same weeds. Weed-free grain strips next to the weedy ones were provided in each case as checks. Each cereal was sown with eight weeds in six replicates. One replicate was used for the excavation work and the other five were harvested at maturity for determinations concerning the development of their top growth. At 5, 22 and 40 days after emergence the plants from both check and weedy strips were excavated and their root systems studied in the usual manner. To demonstrate the results from this experiment some illustrations of actual root systems as well as the data procured from their analyses are presented in figures 2, 3 and 4 and table IV.

The root systems shown in figures 2, 3 and 4 were first separated under water from those of the associated plants, individually analysed, dyed, spread to their natural positions according to the field charts, mounted, carefully drained and permanently preserved in frames. The Searle Grain Company, of Winnipeg, photographed them. Figure 2 represents Hannchen barley (roots not marked) in competition with wild oats (roots marked 1, 2, 3) as they grew in rows three inches apart. Figure 3 represents competition of Marquis wheat (roots not marked) with wild oats (roots marked 1, 2, 3). Figure 4 shows the competition between Marquis wheat (roots marked 1, 2, 3, 4) and wild mustard (roots not marked). The illustrations supply an instant and vivid explanation of the primary cause of losses in crop yield from the weedy fields. Comparison of the statistical data in table IV gives a real meaning of the mutual struggle between the plants, and reveals that both barley and wheat have suffered considerably from competition with wild oats. Barley, however, was much more successful in subduing the weeds

toward maturity as may be seen from the supplementary results from the 40 day stage as given at the bottom of table IV. In this particular case at harvest the weeds hardly produced seed in the plots of barley but were quite prominent in those sown to Marquis wheat.

The data from the same table together with figure 4 show that wild mustard has harmed Marquis wheat to a much greater extent than the wild oat

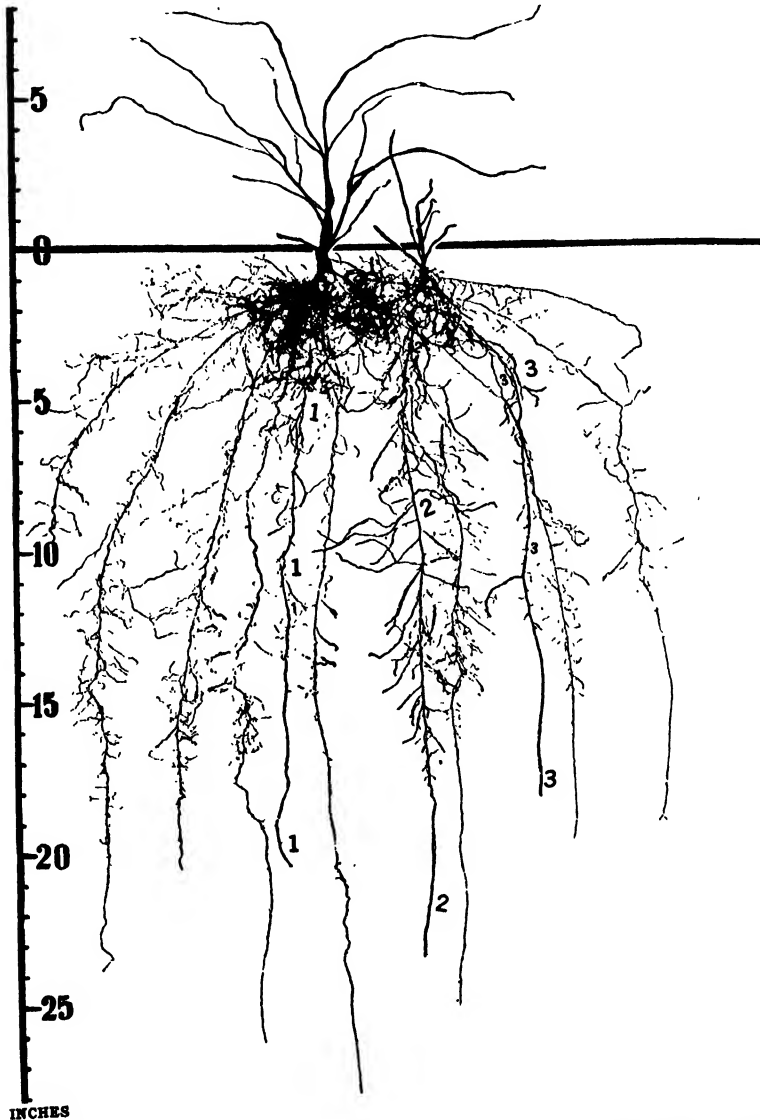


FIG. 2. Root competition between Hannchen barley (left) and wild oats (marked 1, 2, 3), 22 days after emergence.

did. The observations on the top growth in the wheat-mustard competition plots were in full agreement with the statistical data. At maturity the plots were full of rank mustard growth practically obscuring the crop plants. From the economic standpoint the crop was not worth cutting.

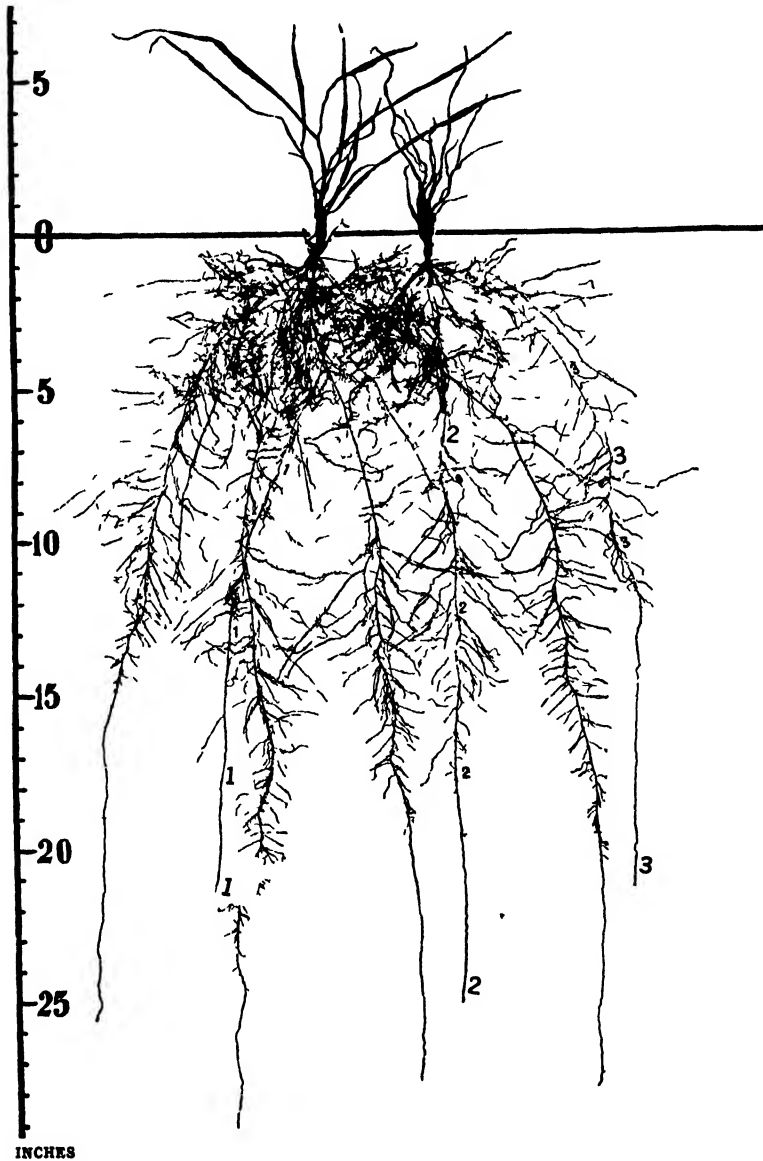


FIG. 3. Root competition between Marquis wheat (left) and wild oats (marked 1, 2, 3), 22 days after emergence,

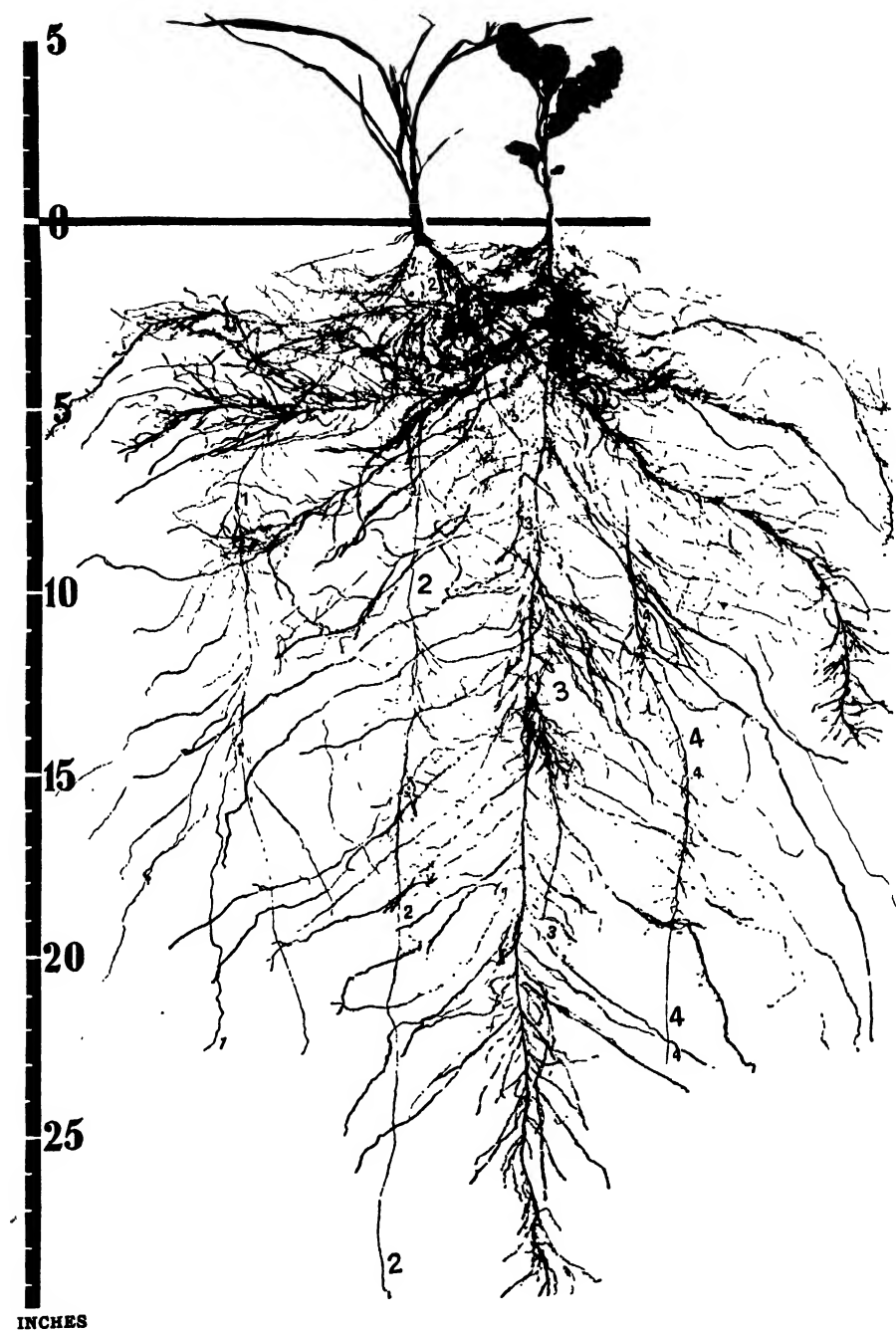


FIG. 4. Root competition between Marquis wheat (left, roots marked 1, 2, 3, 4) and wild mustard, 22 days after emergence.

GENERAL DISCUSSION

The fundamental object in studying root systems always has been to disclose their nature and performance. For the purpose of morphological classification of the root structures as well as the theoretical study of their physiological performance the root systems of plants grown in a greenhouse may be advantageously used and this simplifies the problems. For practical purposes, however, arising in connection with various activities directed toward the improvement of agriculture, the nature and performance of the roots developing under a variety of natural conditions are of real economical importance, as they are the fundamental cause conditioning the proper development of aerial vegetation. Under natural conditions the structure of the soil often is very coarse; in most cases several plant species grow together; their root systems are very extensive and their exceedingly fine rootlets are intimately interwoven; all this, undoubtedly, complicates the problem of root study. However, even under these conditions it is a comparatively easy matter to separate from the soil the coarser roots effecting the anchorage of plants. Yet it is not these coarse roots but the smallest fine rootlets that form and represent the active absorption surface of a root system. Without separating these in an undamaged condition and in sufficient quantity, it is impossible to comprehend the actual functioning capacity of a root system.

The method of work should comply with the coarseness of the medium and at the same time with the fineness of the root structures. The results presented in this paper give some indication of the possibilities of work along this line. The method allows for the extrication of the root system from the ground without touching any root structure by hands or any other hard object until the last soil particle is removed. It is entirely due to this fact that at analyses in water one can see a mass of exceedingly fine rootlets of various orders in a perfectly undamaged condition. In fact not only the fine root branches were observed, but also the area bearing active root hairs as well as the length, frequency and number of the latter, could be fully studied. All the data presented in this paper were secured from material of this nature. That is why it is felt that they show the actual differences between the entire root systems of plants, due either to specific characteristics or to the various intensities of competition inflicted upon them by crowding during the period of growth. These data are used only to illustrate a much greater body of results of similar nature from many other weed species, and grain and forage crops.

In interpreting the data herein presented one should keep in mind that they were obtained from only one soil type and under one set of ecological conditions characteristic of the Plains-Park Transitional zone of the western Canadian prairies. The fact that certain weeds, as well as the cereal and forage crops can grow successfully only in definite districts or soil types, while the others can do so over much greater areas, seems to indicate a differ-

ent amount of adaptability on the part of the plants to various soil and climatic conditions. This however can be ascertained only if similar work is done simultaneously in different places with characteristic soil types and ecological environment. The information thus procured would form a basis for applied plant ecology and give fundamental facts essential to those engaged in crop improvement, in soil management and reclamation projects, in weed control, plant pathology, entomology, melioration and irrigation of land, etc. The work is slow and costly. It requires extreme endurance, quick orientation and broad vision on the part of the technical workers, and an appreciative attitude on the part of the financing institutions.

SUMMARY

Employing a special method devised in 1930 and 1931 in the Weed Research Nursery, at the University of Saskatchewan, a quantitative study of the entire root systems of certain common weeds and crop plants was made under field conditions, in order to determine their competitive powers. The plants were studied under three different intensities of competition.

In one case single plants grew free from competition of any kind, each in the centre of an area 10 feet square. At maturity these produced root systems measuring as follows: Wild oats 3,456,005 inches; Marquis wheat 2,802,821 inches; and Prolific spring rye 3,114,375 inches.

In another case the weeds and crops grew in six inch rows with 18 to 20 plants to a foot. At maturity these produced from 83 to 99 times smaller root systems than the single plants. The corresponding data from this experiment are as follows: for wild oats 38,452 inches; Marquis wheat 34,150 inches; and Prolific spring rye 38,408 inches.

In the third experiment cereal crops were sown in six inch drills with weeds between the rows of the crops. At 40 days after emergence their root systems compared as follows: In Hannchen barley-wild oat competition 7668 to 1401 inches respectively; in Marquis wheat-wild oat competition 6223 to 2356 inches respectively, and in Marquis wheat-wild mustard competition 3309 to 6496 inches respectively.

ACKNOWLEDGMENT

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FLUCTUATIONS IN BIOTIC COMMUNITIES, III. ASPECTION IN A RAVINE SERE IN CENTRAL OKLAHOMA ¹

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This study is the second of a series dealing with aspection and fluctuations in animal populations of wooded areas. The data were collected in connection with a study of prairie uplands in McClain County, Oklahoma (Carpenter, '36b). The topography of the region is characterized chiefly by rolling hills separated by ravines. In some places gullying has greatly increased during the period of heavy grazing prevailing since the latter portion of the last century. The consequent succession and the seasonal aspects of the more distinct seral communities are described.

SUCCESION

General Features

The underlying rock of the area studied is non-glaciated red Permian sandstone. It has been reworked largely, many areas being wind-deposited. Stratification in areas deeply cut by gullying shows that at several periods in comparatively recent geological time ravines at least have been more heavily wooded. Certain relict communities in the canyons of western Oklahoma also support this contention.

Two principal processes, sheet erosion and gullying, cause succession in the region. Both are attributable to the grazing management of the prairie. Large numbers of cattle are pastured and, especially in winter and spring, there are frequent fires. Neither overgrazing nor fire need be considered as "unnatural," but the herds of bison ranged freely and widely, and if a particular area was intensively grazed one year, it would not necessarily receive the same harsh treatment the following year. Fires also were less frequent. At least the consistent combination of both, which the area has experienced almost every season from 1890 until the all too recent improvement in range management, did not exist under primitive conditions. Removal of the basal field cover of grasses has destroyed the smaller ground forms which bind the soil and aid in the accumulation of humus. These gone, the developed soil rapidly erodes leaving the undeveloped soil beneath. Frequently this poorer soil also erodes and is deposited on the fertile floodplains of rivers in the lower areas, decreasing their productiveness. With a decrease in ground

¹ Contribution from the Zoological Laboratory, University of Oklahoma, N. S. No. 151.

cover the water runs off much more rapidly leaving little in the soil for the dry season. The available drainage paths are overloaded, and severe gully-ing results. An appalling amount of surface soil is removed from the area.

The present system of gullies follows the general local system laid down earlier in geological time. This is indicated by the non-worked Permian out-crops which occur as occasional miniature bluffs on either side of the ravines and at some distance from the present edges. The sides of the ravines are

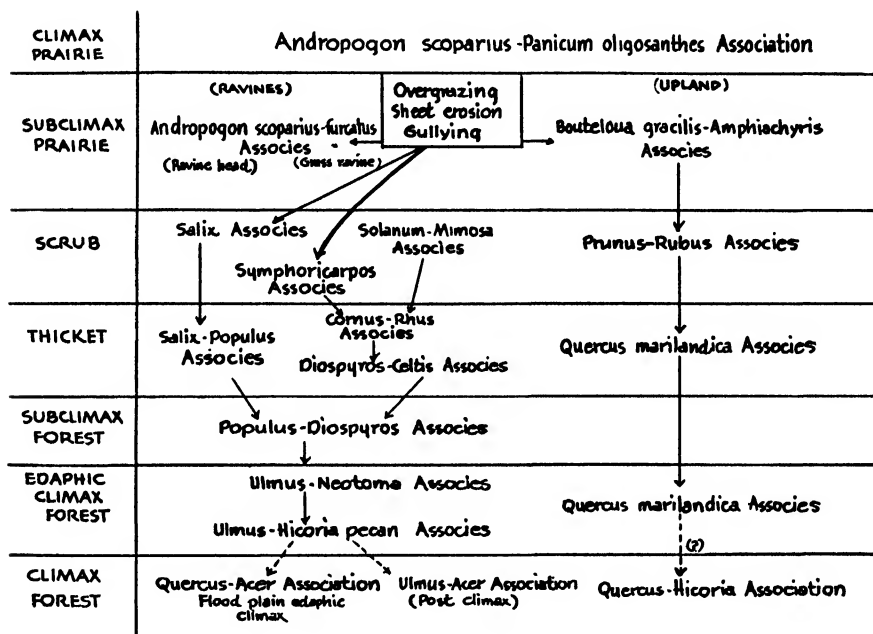


FIG. 1. Upland ravine succession, McClain Co., Oklahoma.

not exactly the same as any previous gullies or ravines, but the latter may influence the degree of slope from the surrounding upland. This factor was found to be rather important in determining the direction of succession in certain cases. As will be pointed out later, a steep slope is usually wooded and a gentle slope is grass covered.

Communities of the Ravine Sere

The details of the structure and aspection in the prairie communities of the upland are being reported elsewhere (Carpenter, '36b). In summary, however, it may be said that they are dominated by *Andropogon scoparius* and *Panicum oligosanthos*, with *Bouteloua gracilis* added in the higher areas (*A. scoparius* losing its importance on certain of these). *Manisuris* (*Rottboellia*) *cylindrica* is added on slopes, and *Andropogon furcatus* and *M. cylindrica* on lower ground.

Disturbed prairie communities. Disturbance of the upland by overgrazing or burning, with accompanying sheet erosion, results in invasion by "weed grasses," forbs, and seasonals. Among the most common are *Bouteloua hirsuta*, *Andropogon virginicus* and *ternarius*, *Vernonia baldwini* and *Amphiachyris dracunculoides*. Together with the more drought resisting species of the usual prairie flora, these constitute an eastward extension of the more westward conditions of mixed- and even short-grass prairies.² The climax species may again invade, and a state of dynamic equilibrium may be considered to exist between these two stages. Many species are common to both and the direction of development at any one time depends upon the amount of immediate disturbance.

Upland thicket communities. Further succession from the "disturbed" stages mentioned above may be caused by gullying and consequent physiographic change, or by the invasion of more weedy plants (*Vernonia*, *Solidago*, etc.) and woody shrubs (*Prunus*, *Rosa*) which may result in an upland scrub stage with very dense thickets 3 to 5 feet in height. *A. scoparius* frequently grows very high (2-4 feet). In certain cases this stage has been observed to be trending toward an upland *Quercus marilandica* associates, which develops very slowly. There is very little undergrowth; the trees are close together, and on clayey soils rarely attain a height greater than 15 feet (see Brown, '31, for an ecological study of this community on sand). Unless removed by cutting or severe fire, this community is not replaced by prairie.

Initial ravine stage. In severe sheet erosion of the uplands the last plants to lose place are the bunch grasses (chiefly *A. scoparius* and *Manisuris*), which remain as clumps, often perched upon little monadnocks after the surrounding soil has been washed away. Further erosion between these clumps, together with erosion in old wagon tracks and cow-paths, are the two factors of greatest importance in determining the exact location of embryonic ravines. Once started they develop rapidly, cutting as deep as five or six feet, while the width may remain as narrow as twelve inches. Water entering these ravines laterally destroys the steep sides rather quickly and on the resulting broken edges such plants as *Vernonia baldwini*, *Solanum rostratum*, *Callirhoe involucrata*, *Artemisia*, and *Mimosa* invade. These are usually succeeded by *Rhus trilobata*, *Vernonia baldwini*, *Solidago* spp. and *Polygonum*. Where moisture is more abundant, *Salix* and *Populus* appear. These may hold the severe physiographic succession in check, or at least temper its advance. They constitute a thicket stage which may endure for long periods.

If the ravine assumes a wider aspect upon gullying, a grass stage may result and retard physiographic succession. If erosion continues, it may be

² The resulting community has been intensively studied from the standpoint of the local distribution of the dominants and their quantitative abundance by Carpenter ('36a). Aspect of the insect forms is also being reported upon (Carpenter, '36b, "Aspect on burned prairie," sect. 7).

succeeded by a *Prunus-Symphoricarpos* stage which will usually give way to the thicket stage.

Midseral stages. If further physiographic succession goes on, and the ravine is widened, a community dominated by cottonwood (*Populus deltoides*), redbud (*Cercis canadensis*), grape (*Vitis* spp.), elm (*Ulmus americana*), and a dense shrub layer of dwarf plum (*Prunus* spp.) and haw (*Crataegus* spp.) develops. Field mice (*Peromyscus*), cotton rats, and squirrels are abundant. The millipeds of the later wooded stages do not come in until logs and stumps other than those of cottonwood are present. The length of life of this community is usually only that of one generation of cottonwoods, for the young *Populus* does not grow well in the shade of the old trees. Dying cottonwoods are usually replaced by the growing elms, and a community dominated largely by the latter results. If these elms are not present in sufficient numbers or do not rapidly assume control of the community by closing the tree canopy where the cottonwoods have fallen, there is a rapid invasion by prairie forms, both plant and animal. This process is at its height during the aestival and serotinal periods where the available moisture is at a minimum. The break in the tree canopy permits a high evaporation rate and succession is very likely to go toward ravine prairie conditions.

It was noted repeatedly that ravine edge slopes of more than 25 per cent gradient were wooded and those of less than 15 per cent were occupied by grass (no cases were found falling between these two points). Two factors of ecological importance may result from this difference. First, the gradual slope with its relatively slower drainage retains the finer particles of soil and as a result is more favorable for grasses. Steep slopes on the other hand lose many of the finer particles, and a soil of very coarse texture results, which is suitable for woody plants. Second, gradual slopes are more exposed to desiccating winds which aid the prairie plants in competition by creating unfavorable conditions for ravine forest species. Where slopes are steep, drying winds pass over the ravine and permit a high humidity in the lower strata of vegetation. These factors are of importance in determining whether the elm will be on hand to assume dominance when the cottonwoods fall.

Grass ravines resulting from invasion and establishment of prairie in formerly wooded ravines are occupied by *Andropogon scoparius* and *virginicus*, *Monarda*; occasionally by *Panicum virgatum* and *Elymus canadensis*; and sometimes by *Baptisia* spp. or *Symphoricarpos*. Old *Smilax* roots are frequently found persisting in these prairie ravines long after all other remnants of the former woodland have disappeared.

Ravine subclimax. The elm stage, which may properly be called an edaphic subclimax in the ravine sere, is characteristic of rather wide ravines. Shrubs and young trees are present throughout early development and there is a concentration of shrubs and smaller trees at the edges, comparable to a

forest edge. In older stages the young trees and shrubs are limited to the ravine edges and slopes, the ravine basin proper being filled by the older trees and *Symphoricarpos* only. One possible reason is that deposits of soils on the ravine bottoms during the spring rains cover and kill many species of small plants and young trees. As a consequence, only the older trees and the hardy, often pioneering *Symphoricarpos* are all that are able to remain. With the retreat of the shrubs to the ravine sides, the very characteristic woodrat also moves to the ravine edges, where the conspicuous houses of brush around old logs are to be seen. A transect made in a rather late stage of this associes gave the following list:

<i>Ulmus</i> (old)	23	<i>Bumelia</i>	4
<i>Ulmus</i> (young)	17	<i>Populus</i>	1
<i>Vitis</i>	39	<i>Quercus marilandica</i>	1
<i>Crataegus</i>	19	<i>Parthenocissus</i>	5
<i>Cercis</i>	6	<i>Fraxinus</i>	2
<i>Prunus</i>	4	<i>Amorpha</i>	4

Present in great numbers, but not in the transect, were *Cornus asperifolia*, *Symphoricarpos occidentalis*, and *Celtis*. Also present were a few specimens of moonseed (*Menispermum*), and persimmon (*Diospyros*). The latter was characteristic of the earlier stages of this associes.

This stage is probably of very long duration, as examination of tree rings of stumps and of increment borings showed that certain of the older trees (elms) were over 150 years old. In the older stands of this community were found also pecan (*Hicoria pecan*), *Quercus macrocarpa*, and walnut (*Juglans nigra*), showing that the trend is eventually toward the edaphic elm-oak forest association of the floodplain (Hefley, '36).

Further physiographic succession. The undeveloped and frequently recently deposited soil of the ravine bottom is sometimes further eroded during and after heavy rains. This results in a ravine within a ravine, and in some instances tertiary ravines may be found. The depressed terraces thus formed are fully protected in most cases by the tree canopy of the levels above. The initial stages of the sere are consequently rather different from those of the primary succession on the upland. The high humidity permits *Salix* to come in rapidly. It is supplemented by cottonwood, persimmon, and by the trees of the upper terrace which have slid down bodily into the new ravine with large amounts of earth about their roots. The wooded ravine subclimax of elm results on these lower terraces. The levels of these communities may be from twenty-five to fifty feet below the original ravine bottom and as much as seventy-five feet from the level of the surrounding prairie.

The forest climax of the sere. Extreme tension often prevents the development of ravines to the wooded stage or the maintenance of this condition. It is obvious that the sere does not lead to the present climatic climax of the region. It appears to be a relict of a former more extensive climax forest in the region. A relict of such a climax, that is, a post climax, is to

be found about sixty miles farther west in Caddo County, where there is an elm-maple community in a deep canyon. A series of transects across this canyon at several places showed that where the canyon was narrow the elm-maple community was present, but that where the canyon widened and permitted the drying winds of the uplands to enter the facies changed very quickly to the type of vegetation more typical of the region. In addition to the dominant trees *Ulmus americana* and *Acer saccharum*, the following species (listed in order of decreasing frequency) were also present rather abundantly: *Menispermum canadense*, *Symphoricarpos* sp., *Celtis occidentalis*, *Cercis canadensis*, *Cornus asperifolia*, *Quercus michauxii*, *Vitis* sp., *Gymnocladus canadensis*, *Morus rubra*, *Bumelia lanuginosa*, *Juglans riparia*, *Juniperus virginiana*, *Rhus toxicodendron*, *Similax* sp., *Acer negundo*, *Quercus macrocarpa*, Chittamwood, and *Sambucus canadensis*. The milliped and phalangiid fauna was also strikingly that of a mesic forest.

ASPECTION

This section deals with aspection and its accompanying fluctuations in several of the communities of the sere. The data are for the period from autumn, 1933 to summer, 1935, during which time the calendar of the biotic seasons was as follows (dates are approximate to one week):

Prevernal	March 15-April	27
Vernal	April 27-June	2
Aestival	June 2-July	29
Serotinal	July 29-Sept.	6
Autumnal	Sept. 6-Dec.	1
Hiemal	Dec. 1-March	15
Hibernal	Dec. 1-Feb.	15

INITIAL COMMUNITIES

Prevernal aspection began slightly earlier in the open communities at the heads of the ravines than on the adjacent sloping prairie, due to protection from winds in the ravine. As early as February 18, chironomids, muscids, and miscellaneous gnats and spiders were active on warm days. Characteristic prevernal insects were *Typophorus canellus* and *Eritettix simplex*. After the prevernal period aspection progressed similarly to that of the sloping prairie.

Activity in the ravine head communities dominated by *Symphoricarpos* and *Rubus* began chiefly as the former came into leaf, when several Diptera appeared. By the middle of April, *Thyanta custator* was abundant, and *Euschistus servus*, *Calocoris norvegicus*, and *Xerophiloea viridis* were also present. The first two forms were invaders from the more mature woodland communities. During the vernal period such plants as *Oxytropis*, *Lesquerella*, *Rosa*, *Verbena*, *Plantago*, *Specularia*, and *Sonchus* became conspicuous. The vernal insects associated with *Symphoricarpos* were *Delto-*

cephalus configuratus, *Macropsis basalis*, *Phlepsius truncatus*, and *Ortholomus jamaicensis*. *Terrapene ornata* also was found active.

The aestival period was characterized particularly by the blooming of *Vernonia* and by the marked abundance of *Syrbula admirabilis*. Lesser insects were *Orphulella pelidna*, *Scolops spurcus*, *Homacmus acnifrons*, *Oncometopia undata*, *Stictocephala inermis*, *Stagmomantis carolina*, *Diapheromera femorata*, *Mermiria maculipennis*, *Xanthippus corallipes*, and *Disostocira carolina*. In the areas of taller vegetation, dominated by *Vernonia*, were many *Mermiria maculipennis*, *Melanoplus bivittatus*, a camel cricket, *Driatura robusta*, and certain Buprestidae. Serotinal forms were at a minimum owing to the extremely dry late summer. Some of the drought resisting forms spent portions of the warmer days sheltered from the sun beneath shrubby vegetation and moved into the sloping and higher prairie during cooler parts of the day. Autumnal forms were miscellaneous Chironomidae and Trypetidae, *Adelphocoris rapidus*, and *Melanoplus bivittatus*. With the coming of winter the population decreased and, as in the sloping prairie uplands, certain individuals hibernated in clumps of grass. Most abundant of these were *Hippodamia convergens* and *Picsma cinerea*.

MIDSERAL COMMUNITIES

The animals of the thicket communities began their activity early in the prevernal period as soon as the more protected trees and shrubs began leafing. In this respect this community is very similar to the corresponding layers of the more advanced elm community. *Typophorus canellus*, *Empoasca radiata*, *Apis mellifica* and many Diptera (including Tipulidae) were active by the middle of the prevernal period, coincident with the blooming of the redbud (*Cercis canadensis*). In the vernal period more *T. canellus* and *E. radiata* appeared, supplemented by *Gypona octolineata*. More abundant forms in the aestival-serotinal periods were *Sinea diadema*, *Ceresa bubalis* and *Mermiria maculipennis*. As the serotinal period advanced, *E. radiata* again appeared, with *Chrysopa* and *Stagmomantis*, and was the outstanding autumn insect. The winter fauna in the earlier stages (*Cornus-Rhus*) consisted of many hibernating individuals of *Aphodius servus* and *E. radiata*, with a few *Nabis limbalus* and *Ischnodemus lobatus*. Several dead *Solubea pugnax* were collected. Later stages (*Diospyros-Celtis*) sheltered *Solubea pugnax*, *Nabis limbalus* and *subcoleopttratus*, *Peribalus limbolarius*, and *Prenolepis imparis*.

RAVINE SUBCLIMAX COMMUNITY

(Tables II, III)

Prevernation began in this community with the first budding of the elms (Feb. 18, 1934; Feb. 21, 1935) and *Symphoricarpos*. Flies (Chironomidae, Muscidae, gnats) and spiders are associated with both the elm and buckbrush. In about a week the elms were in leaf and the early vines had begun

TABLE II. *Biotic Composition and Aspection in the Ravine Subclimax Community. Ulmus-Symphoricarpos-Neotoma Associes*

Perennial Nucleus.

Dominants: *Ulmus americana*, *Populus deltoides*, *Symphoricarpos occidentalis*, *Cercis canadensis*, *Prunus americana*, *Viburnum prunifolium*, *Vitis* sp., *Diospyros virginiana*, *Crataegus* sp., *Fraxinus*.

Predominants: (Virginia deer), (Elk), White footed prairie mouse, Pack rat, White footed wood mouse, Cotton rat, Cottontail rabbit, coyote, Fox squirrel, Oklahoma wolf, Short tailed shrew, Mole, Raccoon, (Black Bear), Opossum.

Fluctuating Predominants: Cardinal, Bluejay, Junco, Hairy woodpecker, (Wild Turkey), Robin, Black capped chickadee, Mourning dove, Harris sparrow, Red shafted flicker, Carolina wren, Bluebird, catbird, Blue darter hawk, Eastern red tailed hawk, Sparrow hawk, Northern shrike.

Hiemal Presocies.

Incidentals: *Euscelis obscurinervis*, *Phlepsius truncatus* and *imparis*, *Blissus leucopterus*, *Chortophaga viridifasciata*.

Hibernal Presocies.

Abundant: *Empoasca radiata*, *Aphodius servus*, *Thyanta custator*, *Nabis subcoleoptratus*, *Sinea* sp.

Incidentals: *Empoasca maligna*, *Peribalus imparis*, *Crematogaster lineolata*, *Nabis propinquus*, and *limbatus*, *Leucotermes flavipes*, *Solubea pugnax*, *Lebia grandis*, *Euschistus servus*, *Draculocephala reticulata*, *Typophorus canellus*, *Cynorta sayii*, *Lutrodictus mactans*, *Tetragnatha laboriosa*.

Prevernal Socies.

Subdominants: *Bumelia lanuginosa*, *Benzoin aestivale*, *Viola rafinesquii*, *Erigeron ramosus*.

Influents: Apidae, Tenthredinidae, Tipulidae, Argynnoids, Hesperidae, *Anassa atalanta*, Pieridae, *Chrysopa*, *Chlosyne lecinia*, *Thyanta custator*, *Empoasca radiata*.

Incidentals: *Entylia bacciana*, *Gargaphia solani*, *Empoasca trifasciata*, *Apion pennsylvanicum*, *Metachroma denticulata*.

Vernal Socies.

Subdominants: *Sisyrinchium granuloides*, *Viola rafinesquii*, *Callirhoe involucrata*, *Vernonia baldwinii*, *Vitis* sp., *Rubus*.

Influents: Bombidae, *Phyllophaga* sp., *Euschistus servus* and *variolarius*, *Danaus archippus*.

Incidentals: *Thyanta custator*, *Gargaphia solani*, *Empoasca radiata*, *Idiocerus crataegi*, *Solubea pugnax*, *Macropsis basalis*, *Catonia pumila*, *Deltocephalus configuratus*, *Scolops spurcus*.

Aestival Socies.

Minor influents: *Euschistus servus*, *Melanoplus bivittatus*, *Solubea pugnax*, *Oncometopia undata*, *Danaus archippus*.

Incidentals: *Deltocephalus configuratus*, *Scolops spurcus*, *Melanoplus scudderi* (nymphs), *Melanoplus differentialis*, *Epicacrus formidulosus*, *Macropsis basalis*, *Mormidea lugens*, *Mermiria maculipennis*, *Arphia simplex*.

Serotinal Socies.

Minor Influents: *Melanoplus differentialis*, *Chrysopa* spp., *Danaus archippus*, *Leio-bunum vittatum*.

Incidentals: *Melanoplus bivittatus*, *Syrbula admirabilis* and *fasciata*, *Eugnathodus abdominalis*, *Mermiria maculipennis*, *Arphia simplex*.

Autumnal Socies.

Subinfluents: Chickadee, Harris sparrow, Yellow and Red shafted flickers, Junco, Downy and Hairy woodpeckers, Yellow breasted chat, Tree sparrow, Carolina wren, Robin.

Minor Influents: *Empoasca radiata*, *Idiocerus crataegi*, *Stictocephala lutea*, *Mormidea lugens*, *Thyanta custator*.

Incidentals: *Xerophloea viridis*, *Calocoris norvegicus*, *Phlepsius truncatus*, *Jassus* sp., *Cicadella hieroglyphica*, *Blissus leucopterus*, *Deltocephalus configuratus*, *Melanoplus ponderosa*, *Typophorus canellus*.

Hibernating (Nov. 4, 1934): *Empoasca radiata*, *Aphodius servus*, *Thyanta custator*, *Empoasca maligna*, *Acutalis* sp., *Prenolepis imparis*.

TABLE III. *Aspection in the Tree Layer. Ulmus-Symphoricarpos-Neotoma Associates*

Prevernal Socies.

Influents: *Empoasca radiata*, Psocidae, *Lepidophorus* sp., *Phyllophaga* spp., *Phalacrus politus*.

Incidentals: *Cicadella hieroglyphica*, *Bruchus obtectus*, *Epitrix brevis*, *Galgupha nitiduloides*, *Crematogaster lineolata*, Chironomidae, *Chariesterus antennator*, *Anthicus* sp., *Trachus vacuus*.

Vernal Socies.

Influents: Tipulidae, *Leiobunum vittatum*, Chermidae, Tettigoniidae (nymphs), *Phyllophaga* spp., *Chauliognathus marginatus*.

Aestival Socies.

Influents: *Phyllophaga* spp., *Cicada septendecim*, Tipulidae, Chermidae, *Chrysopa* spp., *Oecanthus nigricornis 4-maculatus*, Tettigoniidae (nymphs), *Chauliognathus marginatus*.

Serotinal Socies.

Influents: *Phyllophaga* spp., *Cicada septendecim*, *Empoasca radiata*, *Pachybrachys hepaticus*.

Autumnal Socies.

Influents: *Idiocerus crataegi*, *Empoasca radiata*.

to bud. By the end of the month the early migrating birds had appeared and had taken shelter in the ravine thickets and woods. Characteristic insects about the trees at this time were honeybees, sawflies, craneflies, fritillaries, and skippers. Principal birds of this period were the junco, chickadee, tufted titmouse, cardinal, Harris sparrow, bluebird, and quail.

The leaves of the lesser shrubs (chittam, elder, and *Symphoricarpos*) were out with the advent of the prevernal period proper (March 24 to April 1). The redbud was in bloom, and great numbers of Apidae and Andrenidae were attracted. The red admiral butterfly also was present. As the month progressed such conspicuous forms as the pentatomid *Euschistus servus* and the monarch butterfly appeared. Among the ground flowering forms were *Viola rafinesquii* and *Erigeron ramosus*. Many insects, the most abundant being *Empoasca radiata* (table III), were associated with the tree layer, which became important during this period.

Vernal flowering in this community consisted largely of *Sisyrinchium*, *Viola rafinesquii*, *Callirhoe*, *Vernonia*, *Vitis*, and *Rubus*, and was accompanied by bees, wasps, and Syrphidae. Here also were *Chrysopa*, dragonflies from the streams in the ravines, *Plathemis lydia*, and *Xanthippus coralipes*. The aestival period was marked by the disappearance of winter and spring migratory birds, the activity of reptiles (lizards, snakes, and turtles), and the appearance of such large insects as *Melanoplus bivittatus*, *Phyllophaga* spp., *Cicada septendecim*, and Scarabaeidae. About July 22 the majority of the year's crop of cicadas emerged, the nymphal cases being very conspicuous on all ravine vegetation at this time. This species was very characteristic at this stage. The "singing" activity on sunny days began about 5:30 A.M. when the first direct rays of sun struck the trees, and continued until dusk (about 8:10 P.M.). On cloudy days there was very little

singing. The wild plum (*Prunus*) was the principal plant to fruit in this period.

The serotinal period during 1934 was particularly dry and the fauna of all habitats was somewhat reduced by the deletion of the less hardy. On the hotter days certain forms such as *Mermiria maculipennis* were found upon the ground exhausted and nearly dead. No trees in the ravines were killed during the drought.

Shortly after the first of September the autumnal period began. Characteristic forms seen during the earlier portion of this period were *Leiobunum vittatum* (during the day now, as well as at night), monarch butterflies, with *Melanoplus bivittatus* continuing, and *Syrbula admirabilis*, *Stagmomantis*, and the chickadee in addition. By the end of the month the fruits of *Symphoricarpos*, persimmon, chittam, and *Cornus* were ripe, and a week later the leaves of the trees were falling. Birds of this period were the chickadee, red and yellow shafted flickers, Harris sparrow, red-tailed hawk, junco, blue-bird, downy and hairy woodpeckers, tree sparrow, and Carolina wren. *Cnemidophorus 6-lineatus* and *Acris gryllus* were found as late as Nov. 27, 1934, synchronous with the late migrating birds. Within a week (by the first of December) however, winter had begun, and the activity of poikilothermic animals was at a minimum. Movement into hibernation on the part of certain of the insects took place during the latter part of the autumnal period. Species found in hibernation during the late autumnal and during the hibernal socies are listed in table II.

GRASS RAVINE COMMUNITIES

Prevernal activity in the open grass communities in ravines was characterized by *Eritettix simplex* and *Stictocephala lutea*. In the vernal socies *Pachybrachys morosus*, *Stictocephala lutea*, and *Bruchus mexicanus* were present in greatest numbers. Invading from the sloping and low prairie were *Stictocephala*, *Cymus virescens*, *Mormidea lugens*, *Mordellistena lutea*, *Cylindrocopturus nanulus*, *Chariesternus antennator*, *Pachybrachys morosus*, *Typophorus canellus*, *Hippodamia convergens*, and a camel cricket, all species found on typical sheltered prairie. Characteristic plants of this period were many grasses in vegetative stages (*Andropogon scoparius*, *furcatus*, etc.), *Mimosa*, *Baptisia*, *Callirhoe*, *Gaura*, *Erigeron*, and *Specularia*. *Terapene ornata* was active.

The aestival climate caused the more open areas of the wooded ravines, that is, those not covered by a tree canopy, to dry out to such an extent that many of the grass ravine species successfully invaded. Most conspicuous among these invaders were *Vernonia*, *Helianthus*, and some grasses. With them were many insects, supplanting all those of the wooded ravine excepting *Empoasca radiata*, *Solubea pugnax*, and *Scolops spurus*. Invaders characteristic of upland prairie were *Stictocephala lutea*, *Chaetocnema denticulata*,

and the camel cricket. During the serotinal period this invasion was continued. *Pachybrachys morosus* and *Chalepus nervosa* coming in from the prairies. Species peculiar to these open-wooded communities were *Zygo-gramma casta*, *Phalacrus politus* at this level, and several Buprestidae.

Early in the autumn the species present in the grass ravines were *Diapheromera femorata*, *Orphulella pelidna*, and *Syrbula admirabilis* from the upland prairie, and *Idiocerus crataegi* from the wooded parts. Later in the season *Colias philodice* (males and females), *Hesperia montivaga*, *Idiocerus crataegi*, *Cymus virescens*, *Homaemus aenifrons*, *Gargaphia solani* and Chironomidae were collected. *Idiocerus crataegi* was active well into the winter.

DISCUSSION

The seral stages which constitute the ravine succession described above are component units in the local regional complex of communities. As noted elsewhere (Carpenter, '36), certain species are not limited to single seral stages in succession. This is particularly evident when the local range of habitats of such migratory forms as insects is studied during the seasons of the year. While a more complete analysis of the interrelationships of all the communities of the local complex is left to a later paper, the following general statements may be made with respect to the more abundant migratory forms in the complex of the ravine succession communities and the adjoining prairie uplands.

Seasonal migration is most characteristic of insects spending the winter as adults or late instars. In the early spring they are active in the habitat where they spent the winter, and subsequently migrate to their summer feeding and breeding areas. Of the more abundant migratory species studied, about seventy-five per cent had this type of life cycle. The remainder of the migratory species, those apparently shifting the place of their greatest abundance as the year advanced, did not appear as adults until the aestival period. Since adults were never collected during the winter period it is presumed that they spent that part of the year as eggs or early instars. In the remainder of this discussion these forms will be indicated by an asterisk (*).

The species considered may be classified as follows, according to their migration behavior: (1) Species which are characteristically prairie forms, spending the winter in that habitat, and moving into more protected areas during the summer or autumn for shelter from the less clement environmental factors of the upland, or in search for the more succulent food in wooded ravines (for example, *Macropsis basalis*), or in more sheltered prairie (*Pachybrachys morosus*, *Mormidea lugens*): (2) Species which spend the winter in sheltered communities, such as grassy or wooded ravines, and move to the higher prairie during the summer. This is the type of migration observed in the Illinois complex studied by Weese ('24) and others. Examples of the sheltered prairie-high prairie type are *Syrbula admirabilis**

*Orphuella pelidna**, *Melanoplus bivittatus**, and *Calocoris norvegicus*. The wooded ravine-prairie type was exemplified by *Euschistus servus* and *Empoasca radiata*, which moved into sheltered prairie areas during the summer, and by the following species which moved into high prairie: *Tyrophorus canellus*, *Thyanta custator*, *Bruchus obtectus*, *Epitrix brevis*, *Deltocephalus configuratus*, *Solubea pugnax*, *Phlepsius truncatus*, *Sinea diadema**, and *Mermiria maculipennis**: (3) Species which migrate vertically from the duff to the tree strata in the wooded areas, following the seasonal shift in maximum leaf surface: *Empoasca radiata*, *Idiocerus crataegi*, *Leiodunum vittatum*, *Cynorta sayii*, *Cicada septendecim*, *Phyllophaga* (daily), and *Pachybrachys hepaticus*: (4) Another type which was observed in several cases migrated during the seasons of maximum abundance in the principal habitat. Migration seemed to supply an outlet of "overflow" for the surplus numbers. Usually there were some individuals of the species in all habitats during the period of abundance in the principal habitat. Examples are *Phalacrus politus*, *Stictocephala lutea*, *Pachybrachys morosus*, *Scolops spurcus*, and *Homaemus acnifrons** from the prairie areas, and *Chrysopa* from the ravine areas.

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AN ECOLOGICAL BASIS FOR REFORESTATION OF SUB-MARGINAL LANDS IN THE CENTRAL HARDWOOD REGION *

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The Central Hardwood Region extends from Ohio westward through Iowa and south through the western half of Kentucky and Tennessee to the Arkansas River in Arkansas. Within this area, it has been estimated that 55 million acres are wooded. In addition, there are approximately 15 million acres of submarginal, eroding land, unfit for agriculture, which present the enormous task of reforestation in this region. While numerous areas of wornout or gullied lands in the Corn Belt present an important problem, most of the land in question lies south of the southern limit of glaciation and represents the more extensive problem (fig. 1).

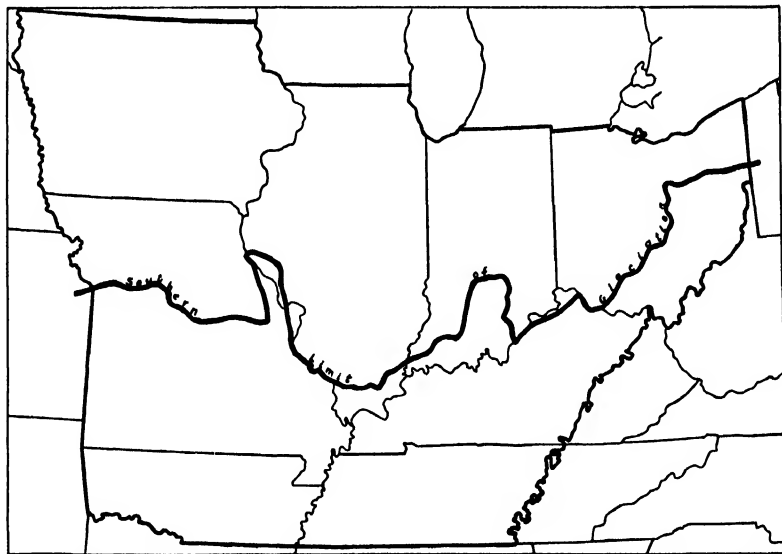


FIG. 1. Region of the central hardwoods showing the southern limit of glaciation.

The reforestation of the denuded lands in the unglaciated portion of the region will be realized both through natural regeneration and planting. For the efficient management of areas of natural reproduction and for successful

* Paper read at the St. Louis Meeting of the Ecological Society of America, December, 1935.

planting, information regarding the distribution of original forest associations, of present forest types, and of succession as affected by climatic factors and to a lesser extent by soil factors, is pertinent.

With the advent of increased interest and development in national, state, and private forestry during the past few years, foresters, while attempting to formulate their planting programs, have recognized the dearth of definite and coherent information relative to the planting problems of submarginal lands. A few plantations were established as far back as seventy-five years ago; but as present day problems were not coexistent with the time of these scattered plantings, they can yield neither sufficient quantitative nor qualitative information. Many of the early plantings were made in part upon the basis of empirical observations or aesthetic values. It seemed to be generally assumed that where certain species once grew well in pure or mixed stands they would grow equally well when planted on lands which had been exhausted by agricultural use. Also, early plantings, as well as later ones, involved to a great extent the use of exotic species. Records of these early plantings are often incomplete or unavailable. This situation excludes any possibility for correlation of planting sites with original and present forest associations.

DISTRIBUTION OF FOREST ASSOCIATIONS

The unglaciated region of the central states has primarily a hardwood forest formation with its component associations. These associations range from extensive mixed mesophytic forests in the east to extensive oak forests with some hickory and pine in Arkansas and southern Missouri, interspersed with fingers of prairie vegetation.

The mixed mesophytic forest, comprised principally of beech, maple, yellow poplar, buckeye, black cherry, ash, chestnut, basswood, white and northern red oaks, is largely confined to the valleys of areas of sharp relief. In general, these occur in parts of southeastern Ohio; in unglaciated southern Indiana and Illinois; in eastern Kentucky, including the "knobs" surrounding the "blue-grass"; in eastern Tennessee; and in the dissected loessial bluffs east of the Mississippi River in both Kentucky and Tennessee. Very limited areas also exist in Crowley's Ridge in eastern Arkansas and in southeastern Missouri. The type develops best in coves and valley bottoms, and on protected slopes where there is a well aerated soil with a fairly constant supply of moisture and high relative humidity. In places somewhat more poorly drained, beech and maple may become the predominant species of the association.

When either clear or selective cutting is done in the mixed mesophytic forest and not followed by cultivation or grazing, the same forest association often returns with the species possibly occurring in different relative percentages. However, near the tension zone between the mixed mesophytic forest and the oak-hickory or other dry types on the upper slopes, more often the

more xeric species return. Upon abandonment of cutover lands following fires, grazing, cultivation, or any combination of factors which destroys the forest ground cover, litter, and soil structure, there results in most cases a development of a more xerophytic association of oak, oak-hickory, oak-pine, or pure pine.

Oak, oak-hickory, oak-chestnut, oak-pine, or pine types have occupied and still occupy the dry ridge tops and excessively drained upland flats. Following abandonment of cutover lands, the factors of the environment are such that only the most xeric oaks, hickories, and pines form the pioneer forest associations. These associations have been greatly extended in area at the expense of the more mesic ones since the early settlement operations of the white man in the region began during the latter part of the eighteenth century. This extension of types has been progressing more rapidly during the last half-century.

Swamp forests of the region occur on stream bottom lands and poorly drained upland flats. These areas are largely agricultural and will seldom be classed as submarginal lands.

Of all the species of possible use in planting occurring naturally in the region, the southern yellow pines—shortleaf (*P. echinata*), pitch (*P. rigida*), and Virginia (*P. virginiana*)—seem to reproduce best on abandoned lands. Loblolly pine (*P. taeda*) also occurs naturally in southern McNairy County, Tennessee, where it reproduces well. In southern Ohio, the first three species are found in association, or singly in pure stands, or mixed with hardwoods. In Kentucky, all three species occur generally south and east of a line drawn through the eastern edge of the "blue-grass" or the western edge of the Cumberland Plateau; but west of the line only Virginia pine has been observed in any abundance. Virginia pine is distributed throughout the "knobs" region and in the western coal field about Dawson Springs. West of the Cumberland Plateau in Tennessee, pine is limited to a few isolated areas of shortleaf and Virginia pines, principally in the region of the Tennessee River on outcrops of the Mississippian and Cretaceous formations, and to small areas of loblolly in McNairy County. Southern Indiana contains only Virginia pine in very local occurrence. In southern Illinois, shortleaf pine is confined to small stands in Union County, near Wolf Lake, and in southern Randolph County. Likewise, only shortleaf pine occurs in southern Missouri and northern Arkansas. However, it occurs intermittently over extensive areas of the same geological formation. In the original forests, due to the prevalence of more tolerant hardwoods, the native southern yellow pines were largely confined to restricted areas on ridges and upper exposed slopes. After the opening up of the hardwood stands by settlers, pine reproduction occurred wherever seed was available or trees were transplanted near buildings, explaining in part the isolation of many stands.

It may be observed that the distribution of pines in this region, with the

exception of Virginia pine, is almost universally limited to areas of residual sandstone soils and cherty mantle. Some investigators attribute this phenomenon to the damping-off of seedlings in the early stage on residual limestone soils, explaining that the fungi develop better in media with high available calcium. It, no doubt, is more than a mere coincidence since the relationship has been also noted in numerous nurseries where pulverized limestone was applied to test seedbeds. Most of the seedlings turned brown and withered shortly after germination. Possibly the correlation will be explained eventually on the basis of physical conditions of the soil which affect soil moisture and aeration or on the basis of a direct physiological effect of basic ions. The difficulty in establishment apparently comes in the period of early seedling growth as trees planted on limestone soils seem to develop quite as well as elsewhere.

Another example of distribution of a species limited by soil factors is found in the eastern red cedar (*Juniperus virginiana*), an excellent nurse species. Throughout this region it occurs on residual limestone soils, limestone outcrops, and residual soils derived from sandstones impregnated with calcium carbonate. The factors which may be significantly correlated with this limited distribution are not yet clear. In the seedling stage the species seems to be very tolerant to low light intensities, but often dies later in the dense shade of hardwood stands. Probably for this reason, the best stands exist on lands too frequently subjected to high fluctuation of soil factors for reproduction and rapid establishment of hardwoods. Like the pines, red cedar establishes itself well in old pastures and on bare areas which afford extremely adverse conditions, and when planted grows satisfactorily on well drained acid soils.

White pine grows in limited areas of the central states. Several trees occur in protected places in northeastern Iowa as far south as Muscatine, in Illinois as far south as LaSalle, and in Indiana as far south as Turkey Run State Park. In Ohio larger isolated groups of trees extend from Lake County, northeast of Cleveland, to Monroe County in the southeastern part of the state, intervening ones occurring in southern Ashland and western Coshoc-ton counties. An extensive area in Kentucky, east of the "blue-grass," centering in Wolfe County and extending into the counties of Lee, Estill, and Menifee, contains native white pine in admixture with many species of mesic hardwoods in valleys and on protected slopes, and less frequently with pitch and shortleaf pines on drier sites. Locally, white pine often makes up a high percentage of the stand and is commercially important. In openings where forest soil and cover conditions have been not too greatly deteriorated, reproduction is common.

Other native northern conifers appearing in the central states are hemlock, larch, and white cedar. Cypress occurs in swamps and river bottomlands as far north as southern Indiana; but, along with the northern conifers

just mentioned, may be dismissed from serious consideration in a planting program that must deal largely with eroding, abandoned lands where frequent fluctuations of many site factors—primarily soil moisture, soil and air temperature, and relative humidity—are extreme.

In summarizing the distribution in the central states of northern and southern coniferous species which have been and will continue to be involved in forest planting in varying degrees, it may suffice to show on an outline map of eastern United States the southern limit of northern species and the northern limit of southern species (fig. 2). It may be noted that the northern

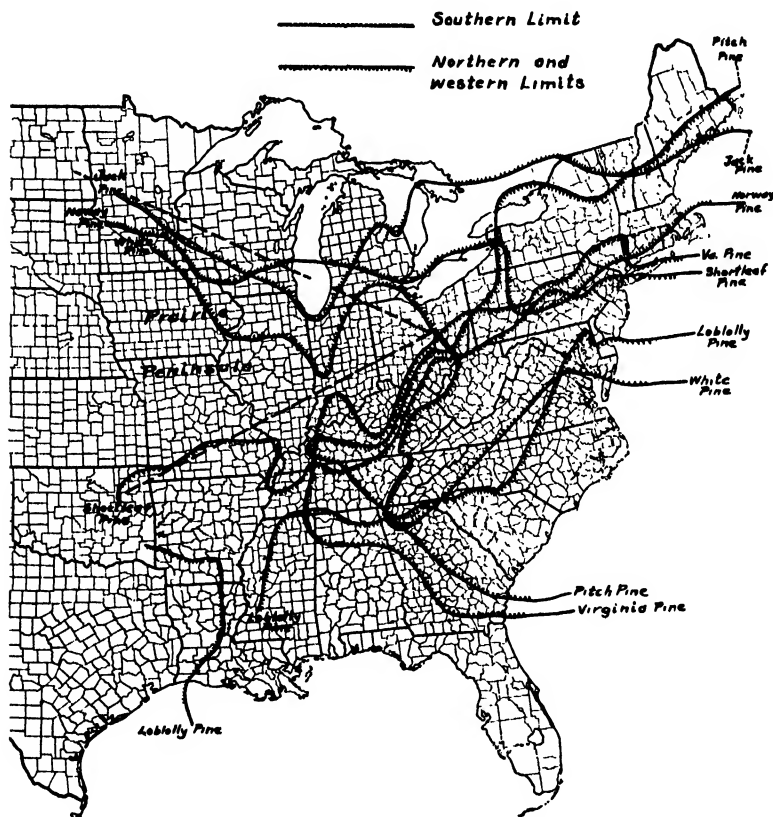


FIG. 2. Southern limits of northern pines and northern limits of some southern pines. The approximate boundary of the "prairie peninsula" is marked by the broken lines.

conifers appear chiefly in the eastern portion of the region. In this margin of their range they are mainly confined to protected slopes and valleys where sufficient soil moisture and high relative humidity favor reproduction and growth.

Certain factors or their various combinations operate in limiting southern

species in their northern extension and northern species in their southern extension. The general direction of the line of the southern limit of the northern conifers is northwest and southeast, while the general direction of the northern limit of the southern conifers is northeast and southwest. The intervening space, whose apex falls roughly in central Ohio, is known as the "prairie peninsula," which has been so aptly described by Transeau ('35). This peninsula is so named because of the frequency of occurrence of prairie areas. Its persistence has been due largely to climatic characteristics, certain measures of which are rainfall-evaporation ratios, mean relative humidity for the summer dry period, and both seasonal and yearly distribution of precipitation (fig. 3). It may be noted that the belt delimited by rainfall-evaporation

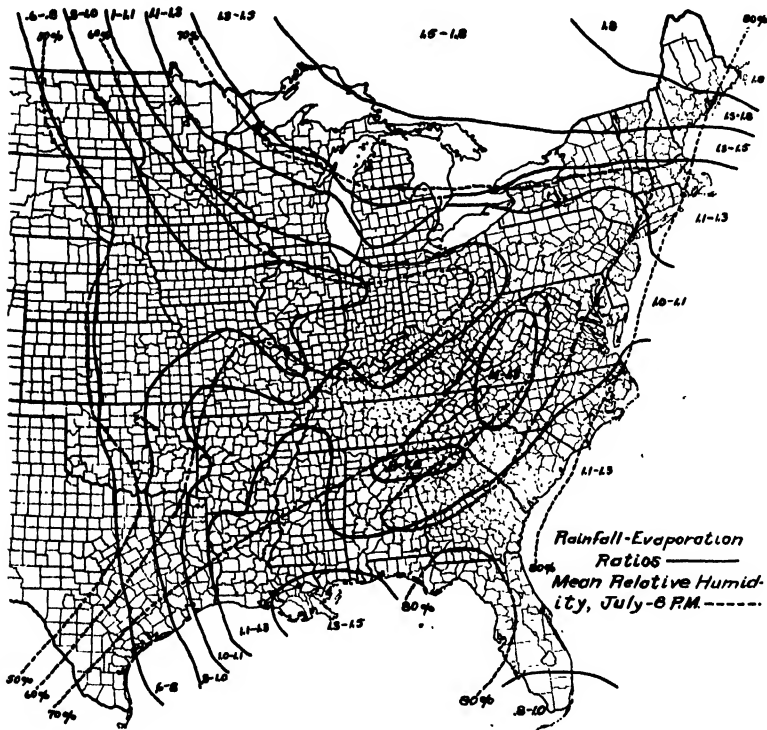


FIG. 3. Rainfall-evaporation ratios and the midsummer mean relative humidities. (Rainfall-evaporation ratios after Transeau; relative humidities after Atlas of American Agriculture.)

ratios .8 and 1.0 is approximately coincident with the limits of the prairie peninsula. Also, the line passing through points of 60 per cent mean relative humidity for July is closely coincident with the limits of the prairie peninsula. Still another "shore line" correlation is that the southern limit of the northern conifers approximates the location of a line representing an average annual snowfall of 40 inches. (fig. 4).

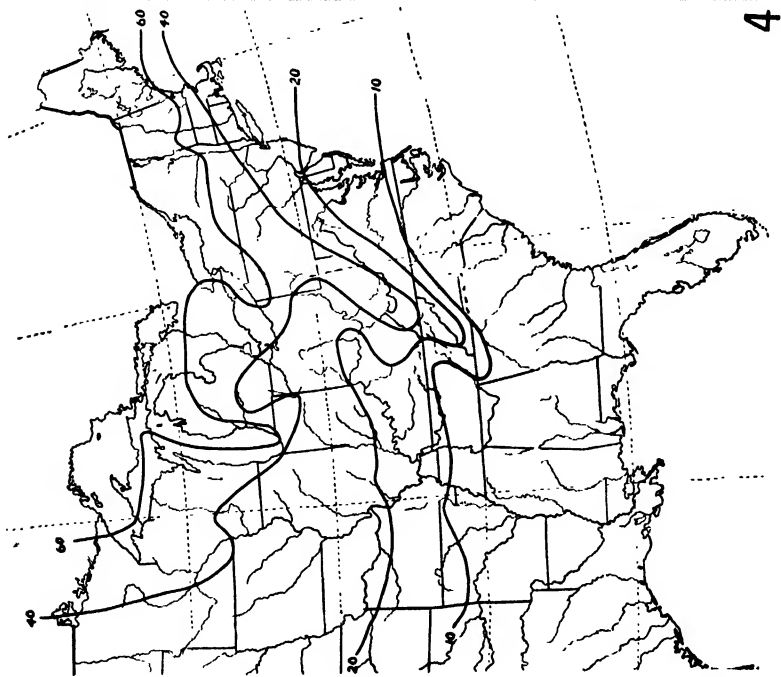


FIG. 4. Snowfall in inches. (Data from Atlas of American Agriculture.)

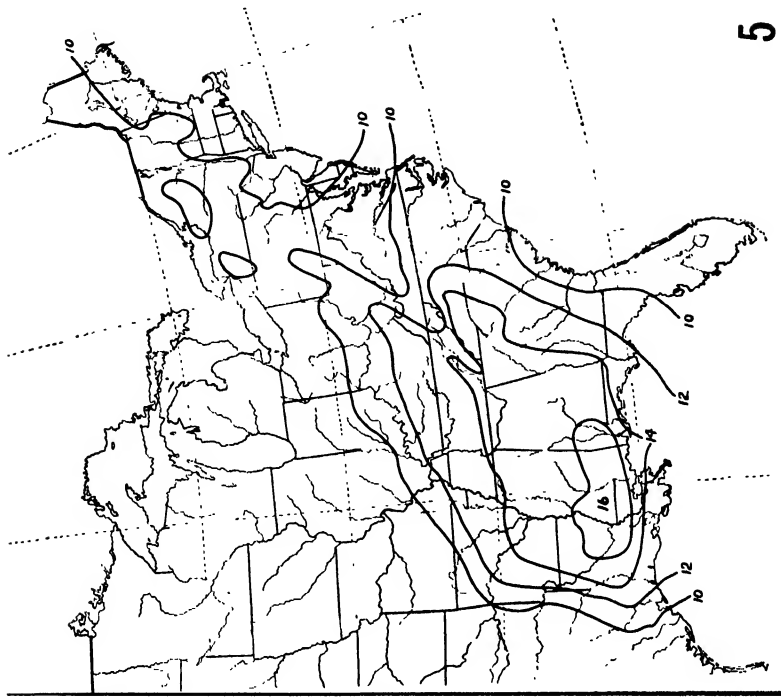


FIG. 5. Winter rainfall in inches. (Data from Atlas of American Agriculture.)

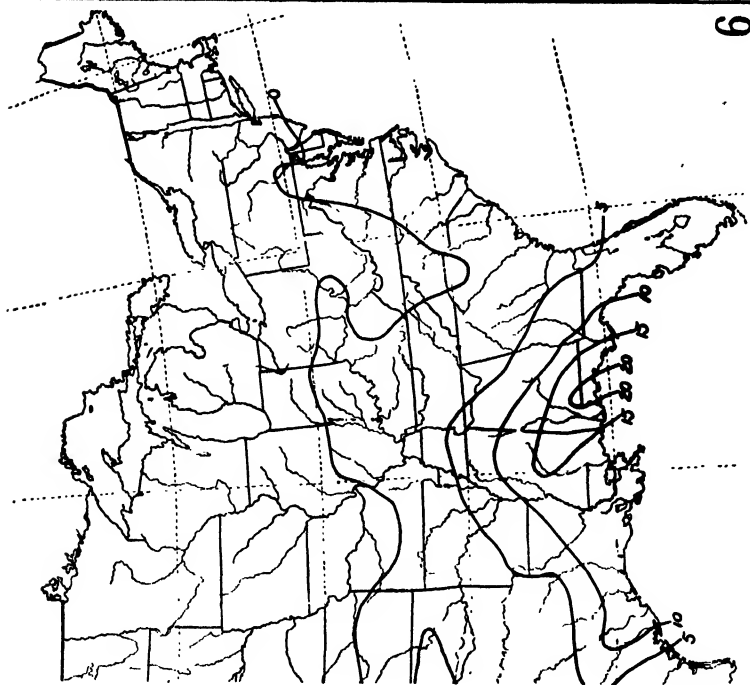


FIG. 6. Number of excessive rainstorms which may be expected to occur in January over a period of thirty years. (After Yarnell.)

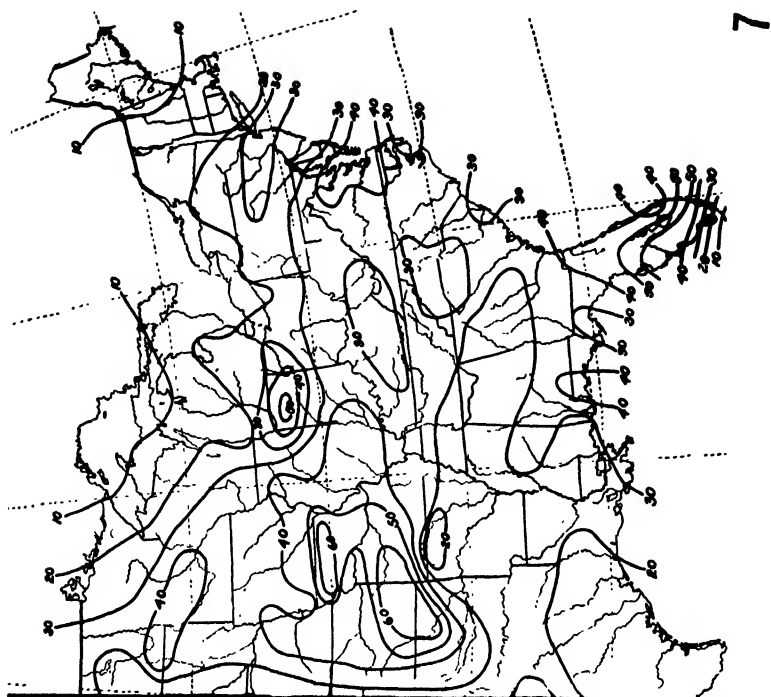


FIG. 7. Number of excessive rainstorms which may be expected to occur in June over a period of thirty years. (After Yarnell.)

Figure 5 shows the distribution of winter precipitation of 10 inches and above for eastern United States. It is evident that the southern portion receives by far the greater amount. It is also significant that the line representing 10 inches of winter precipitation borders the dry prairie peninsula on the south. A more uniform distribution of annual rainfall, as well as heavier rainfall in the southeastern forests than in the prairie peninsula, favors better ground water and soil moisture conditions and higher relative humidity, and promotes forest reproduction and growth. Yarnell ('35) has prepared an excellent series of maps of the United States showing the number of excessive rainstorms which may be expected to occur in each month during a period of thirty years. Two of these maps (figs. 6 and 7) are of particular interest since they show, respectively, excessive rains for mid-winter and for the mid-growing season, January and June. In the prairie peninsula there are none of these rains shown to occur in thirty years in January; but south of the prairie they begin and increase in number to the Gulf of Mexico. On the other hand, the June map shows the greatest number of excessive rains in thirty years to occur in the prairie states. As these rains, which result in heavy run-off and which simulate much less effective rainfall, come during the season when the greater portion of the annual precipitation falls in the prairie, too little water percolates into the soil to tide most tree seedlings over late summer droughts and periodic dry years. Although the excessive rains in the southeastern forests for January and June are not comparable in number, no such great seasonal differences as those existing in the prairie peninsula are noted. The reader may profitably peruse the entire series of maps by Yarnell for further details of distribution of excessive rains.

It may be pointed out that most of the submarginal land within the unglaciated area of the central states is in the northern edge of the range of the southern conifers. The eastern portion of the region, that is, eastern Ohio, Kentucky, and Tennessee, lies within the margins of the ranges of both northern and southern conifers, the area being a tension zone for each.

SELECTION OF SPECIES FOR PLANTING

Since most of the submarginal land of the Central States lies partly in the transition zone between the central hardwoods and the southeastern coniferous and hardwood forest, the difficulty of selection of species for planting is accentuated.

In planning for the reforestation of submarginal lands, definite objectives should be kept in mind. Certainly, the immediate needs of a region should be stressed first and most. In the extensive planting program which is now being initiated, consideration should be given to bare areas first, for the establishment of an early forest cover for erosion control, improvement of soil conditions, and retarding of water run-off. Because of these objectives, there should be set up a standard based upon qualifications of species to meet

the needs for establishing such a forest cover. Such qualifications should include: (1) ability to endure the "shock of transplanting" on submarginal lands, (2) ability to reproduce on submarginal lands, (3) growth rate as a function of time in which a cover may be produced, (4) production of a canopy through which enough light will filter for development of a ground cover and tree reproduction, (5) low cost of seedling production, (6) value as a litter producer with improvement of soil, and (7) commercial value of the final crop. It is understood that the relative importance of these qualifications may vary with planting sites and with the purposes of planting.

CONIFERS VERSUS HARDWOODS

From observations made on the natural reproduction of pioneer forest associations on abandoned lands and in plantations in the unglaciated area, it has been well verified that the less exacting of the conifers become established more readily under adverse site conditions than do most hardwoods. On the deteriorated soils, early increment of these conifers greatly exceeds that of the hardwoods, with the possible exception of black locust. Upon these premises it is safe to confine planting in general to coniferous species.

As before stated, the forests of the region are primarily a hardwood formation. Markets have been established for hardwood species in the industries which are dependent upon them throughout the region. To attempt to change permanently the general physiognomy of the forests would be folly. To attempt to produce the softwoods to compete in the markets with regions already producing them would also be folly. It should be recognized that reforestation with conifers in this connection is a means of hastening restoration of the hardwood forests through soil improvement and cover establishment. However, it may be desirable to introduce yellow pines for permanent management as oak-pine forests on the poorer, drier slopes of the region, which never were and never will be good hardwood sites. Particular reference is made to such areas as are found in the Ozark region of southern Missouri and northern Arkansas, where hardwood forests are composed mainly of the less valuable post, black, and black jack oaks.

It will sometimes be feasible to do a limited amount of planting of hardwood species on good soils in bottomlands and coves, and on protected slopes of the unglaciated region. If such planting can be executed successfully, a number of stages in the succession from the nurse crop of pines to the hardwood forest may be eliminated. Since the motive back of most hardwood plantings is production of valuable products as may be obtained from black walnut, yellow poplar, white and red oaks, relatively few species are being planted. These are all mesophytic species with tap roots which sustain much injury in the processes of seedling lifting and transplanting. Too often, failures have resulted in plantations on over-drained, exposed areas as a result of the limited root absorbing surface of the seedlings. Field seed spot-

ting of the larger fruited species is being more widely practiced to eliminate handling of seedlings.

The success of forest plantings is to a great degree dependent upon the development of planting stock in the nursery. Since the establishment of new federal and state forest nurseries in the central states, both permanent and temporary, many ecological problems in nursery practice have developed. These have resulted directly or indirectly from poorly aerated, heavy soils or a deficiency of the mineral elements essential for plant growth. The cause and effect relationships existing between soil conditions and chlorosis, early stagnation, and heavy loss of seedlings from damping-off fungi need further investigation. Adverse soil conditions have caused especially heavy losses among the pines and black locust.

NATIVE VERSUS EXOTIC CONIFERS

Final decision regarding the choice of indigenous or exotic species for forest planting in this region should be made only after due consideration has been given to the relative degrees of success of both in plantation. Although final success of any planting cannot be determined until maturity, certain responses of planted species to their environment during the early years of establishment, and growth characteristics are criteria upon which certain evaluations may be based. At least, unpromising reforestation species can be discarded.

In the northern states of this region such species as Norway spruce, Scots, Corsican, Austrian, jack, and Norway pines have been used extensively in plantation. This general reliance upon exotics for reforestation in this region is certainly traceable to the European influence upon early American forestry. At present, the ratio of exotic to native stock produced for field planting is being decidedly lowered.

In establishing a forest cover by planting it is desirable to use species which at a later age will reproduce abundantly under highly fluctuating site factors; otherwise, the task of replanting the area probably will arise after harvesting the first crop. Observations made in the unglaciated areas of many twenty- to thirty-year old plantings and older isolated trees of exotic species, which are producing viable seed in abundance, revealed that reproduction is limited to Scots and jack pines. Occasional seedlings of these species are establishing on protected areas only where there are good soil moisture conditions or the soil approaches that under forest influences. The poor reproduction of planted exotics indicates strongly the futility of depending upon these species either for the continuance of a forest cover until native species replace them through succession or for the extension of a forest cover beyond the limits of plantations. The experience of nurserymen has shown that seedlings of northern evergreens in seedbeds are severely damaged in this region by exposure to long periods of direct sunlight accompanied by high temperatures at the soil surface.

To insure a regeneration of our more desirable hardwood forests following planting of conifers, the site conditions must be altered to the extent that hardwood seeds will germinate and seedlings survive beneath the canopy. The exotics most commonly planted—Norway spruce, Scots, and Norway pines—produce dense foliage and canopies upon closing of the crowns. The shade is intensified under these stands, which usually show only slight differentiation of crown classes. The condition is especially true of the Norway pine. Beneath each of these in older plantings the ground is almost devoid of vegetation, either herbaceous or woody. Starvation of seedlings is probably one cause. The thick, slowly decomposing litter, which forms a poor seed-bed, may be a further limiting factor. White pine is the only indigenous species used for planting which produces dense shade and heavy litter, equal to those of the exotics, while in contrast with them this species develops excellent differentiation in crown classes. Shortleaf, pitch, and Virginia pines produce a thinner foliage; and in plantation as well as in natural stands, there is often a ground cover comprised of herbaceous and shrubby species and reproduction of hardwoods and the pines. The desirable two or three-story forest is thus developing.

Black locust is being planted extensively over a wide range of soil types for erosion control. On the lighter, better drained soils, site improvement is often surprisingly rapid. In many six to ten-year old plantings in the region, excellent reproduction of other hardwoods has become established.

The production of planting stock of the exotics involves greater expense than that of the native pines. Generally, the planting stock of the exotics used in this region is three years old, seldom two, and often it is four years old. It is useless to enumerate the phases of nursery work which become costly in the time required to develop these transplants. In the northern states of the region, men who have planted shortleaf, pitch, and loblolly pines prefer 1-1 transplants. Farther south, 1-0 seedlings are almost universally planted, where the final cost of production is approximately one-fifth of that for the exotic species.

Recovery after damage by fire, grazing, and insects varies with species. None of the exotics considered here are known to sucker or sprout following severe injury by the agencies mentioned; but it is common knowledge that shortleaf and pitch pines develop new shoots from adventitious buds after damage, and that seedling sprouts often grow into well formed trees.

Although species most suitable for a quickly developing forest cover are of first consequence, especially for erosion control planting, attention should be given to the relative values of the final planted crops. The real commercial value of a species in any region does not depend wholly upon its wood characteristics, but also upon a certain scale of production which will supply the demands of regional wood-using industries. It does not seem advisable to introduce foreign species or native American species from regions far beyond the range of our central hardwoods and the associated pines in an at-

tempt to create new local markets or compete with production of the exotics in their ranges, especially when we have so many valuable native species in the region.

Within the respective ranges of the native conifers—shortleaf, pitch, Virginia, loblolly, and white pines and red cedar—the choice of species for planting should be based first upon consideration of their responses to site conditions, and second upon their commercial importance.

Until we can secure substantial data from mature stands of carefully planned experimental plantings, we are only justified in making large scale plantings on the basis of ecological principles applied to the native species of the region.

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ECOLOGICAL OBSERVATIONS UPON THE ENEMIES OF *CECROPIA*, WITH PARTICULAR REFERENCE TO ITS HYMENOPTEROUS PARASITES¹

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INTRODUCTION

Within the Chicago area near Summit, Illinois, there is a level prairie community supporting scattered clumps of black willow, box elder, and wild cherry. These trees were found to be heavily infested with cocoons of *Samia cecropia* (Linnaeus), the infestation being reasonably constant from year to year. The writer became engaged in a study of the feeding interrelationships existing between these trees, the Cecropian larvae, and the involved chain of hymenopterous parasites and hyperparasites (Marsh, '34), and this opportunity is taken to discuss briefly certain general aspects of the problem, *e.g.* the biotic balance between moth, predators, and parasites.

METHODS

In collecting the material for this study, the cocoons were kept in three separate groups: (a) those found on the ground—chiefly beneath brittle-stemmed willow trees, (b) those spun from the ground to a height of fifteen feet, and (c) those spun from fifteen feet to thirty-five—the upper limit of cocoons in this region due to the absence of high trees. Age or condition of cocoon made no difference in the uniform sampling of the area. Thus the regulatory factors of several years were determined. The separation into groups according to the stratum occupied was made in order to learn the vertical spread of the factors involved.

The life-history details of the host and parasites were learned from much observation and collection in the field and from laboratory study. In the latter the ichneumonids and chalcids were reared in test tubes lightly stopped with cotton. Honey diluted with an equal part of water proved the most successful diet for the adults.

¹ Throughout the course of this work I have had the advantage of counsel from Dr. C. L. Turner (Northwestern University). It is also a pleasure to acknowledge the criticism of Dr. Orlando Park (Northwestern University), and I am especially indebted to the following taxonomic experts, J. M. Aldrich, R. A. Cushman, A. B. Gahan, C. L. Metcalf, and C. F. W. Muesebeck for their care in determination of insect material.

ECOLOGICAL OBSERVATIONS

A quantitative analysis of the biological influences acting upon the Cecropian cocoons is illustrated in table I. The table represents the results

TABLE I. A general survey (figured in percentage) of 2741 cecropian cocoons collected in the Chicago area in March. I. Cocoons found lying beneath the trees on the ground. II. Cocoons which had been spun from the ground up to a height of about fifteen feet. III. Cocoons which had been spun in the trees at a height of about fifteen to thirty-five feet

Situation of cocoon	Pupa alive in cocoon	Adult emerged	Adult unable to push through valve	Adult dead in pupa case	Pupa destroyed by bird	Pupa destroyed by mouse	Pupa dead from unknown cause	Larva or pupa destroyed by ichneumon fly	Larva destroyed by tachina fly	Larva dead from unknown cause	Cocoon crushed	Scorched by grass fire	Number of cocoons in each group
I	14.3 ♂ 36 64	37.6 ♂ 53 47	0.2	0.8	1.9	14.9	4.1	13.6	1.3	2.2	8.7	0.4	516
II	35.5 54 46	17.2 49 51	0.5	0.3	2.6	6.0	2.1	25.8	4.3	4.8	0.9	None	1827
III	52.3 53 47	8.1 34 66	None	None	8.8	None	3.3	20.0	0.7	6.8	None	None	398
Average for all groups	33.6 52 48	19.7 49 51	0.3	0.3	6.8	3.8	2.5	22.8	3.1	4.4	2.6	0.1	2741

obtained from a dissection of 2741 specimens. The feeding interrelations discerned in this study are given in figure 1. From these two groups of data certain interesting facts may be noted. Thus the ichneumonid *Spilocryptus extrematis* (Cresson) appears to be one of the most important influences in regulating the emergence of the moth, destroying 22.8 per cent of all cocoons. Again, the birds (Hairy Woodpecker and Downy Woodpecker) were second with a destruction of 6.8 per cent, the mice (Meadow Mouse and White-footed Mouse) were third with a destruction of 3.8 per cent, and finally the tachinid was fourth, destroying 3.1 per cent of the Cecropian cocoons.

In the Chicago area *Cecropia* begins to spin about the middle of July. From the time the first mature larva surrounds itself with as much as a thin shell of silk, up to the time when the last pupa case has hardened, about the end of August, the moth is open to attack by its chief enemy *S. extrematis*. The abundance of *Cecropia* in the area studied can be imagined from the finding of nineteen cocoons in a single cluster on a young black willow tree,

while as many as 253 old and new cocoons were found on single adult willows. Still, a casual visitor in the region would not suspect their presence due to the rapid leaf replacement by the willow and box elder, and to the habit of the larvae while feeding, of scattering over the entire food plant. Table II lists

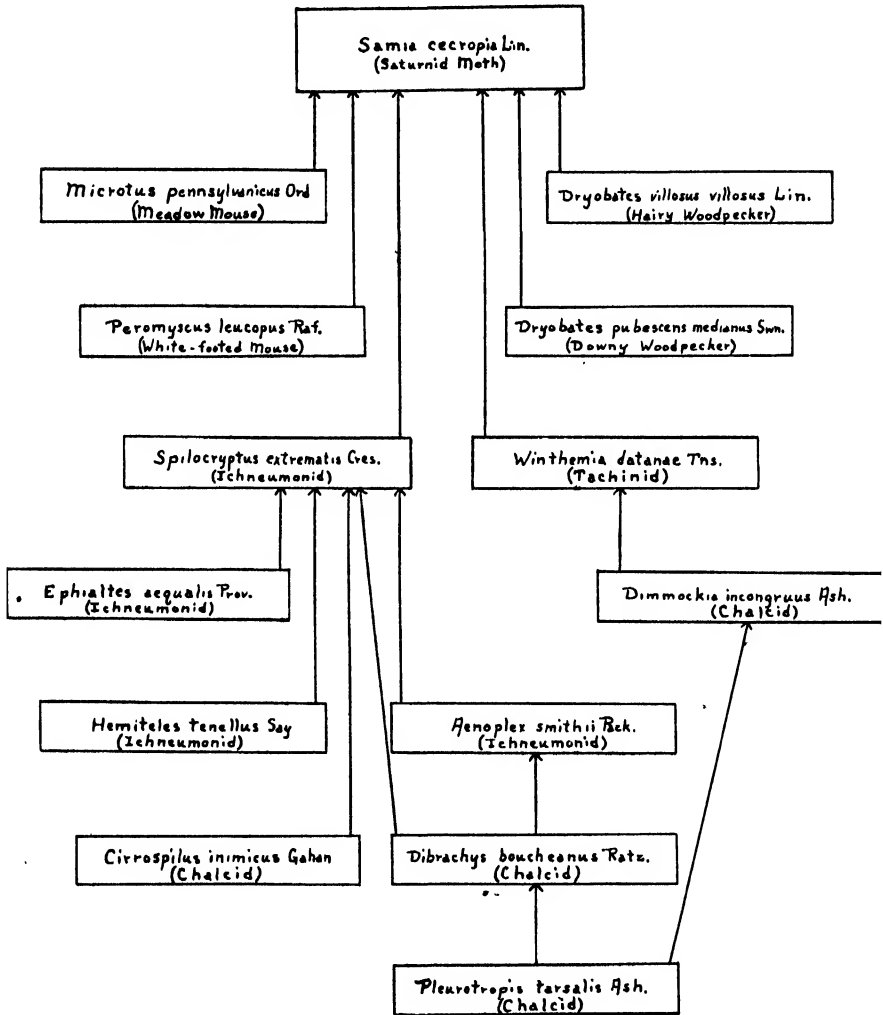


FIG. 1. Diagram of the feeding interrelations discerned in the willow-Cecropia community.

the food plants of Cecropia in this region in graduated series from most stimulating to least stimulating as judged from the abundance of cocoons found on these plants.

TABLE II. *Food plants in the Chicago area from which cecropian cocoons were collected, listed in the order of the number of cocoons found on each species of plant*

Scientific name	Common name
<i>Salix nigra</i>	Black Willow
<i>Acer negundo</i>	Box Elder
<i>Acer saccharinum</i>	Silver or Soft Maple
<i>Prunus serotina</i>	Wild Black Cherry
<i>Populus balsamifera</i> var. <i>virginiana</i>	Cottonwood
<i>Syringa vulgaris</i>	Cultivated Lilac
<i>Maclura pomifera</i>	Osage Orange
<i>Rosa</i>	Cultivated Rose
<i>Arctium lappa</i>	Burdock
<i>Quercus macrocarpa</i>	Bur Oak
<i>Quercus alba</i>	White Oak
<i>Gleditsia triacanthos</i>	Honey Locust
<i>Ulmus americana</i>	American Elm
<i>Rhus toxicodendron</i>	Poison Ivy
<i>Catalpa speciosa</i>	Catalpa
<i>Polygonum hydropiper</i>	Smartweed
<i>Malus ioensis</i>	Wild Crab Apple
<i>Crataegus</i>	Hawthorne
<i>Aster ericoides</i>	Heath Aster
<i>Cannabis sativa</i>	Hemp
<i>Ambrosia artemisiaefolia</i>	Roman Wormwood
<i>Ribes floridum</i>	Wild Black Current
<i>Ambrosia trifida</i>	Great Ragweed

THE FIVE-LINKED CHAIN

In figure 1 it will be noted that *S. extrematis* in turn served as the host of five parasites. However, attention will now be directed to the central chain leading through *S. extrematis* which, in this study, gives the best case of hyperparasitism, ending with the accidental quaternary parasite (Smith, '16) *Pleurotropis tarsalis* (Ashmead). In this case *Cecropia* is the primary host. It is possible that *S. extrematis* is attracted to its host by the odor of freshly spun silk. As soon as cocoon spinning has progressed to a thin-shell stage, females of the ichneumonid have been observed coming up the wind to it as Canthon beetles follow up wind to fresh horse droppings. The ovipositor is thrust through the cocoon, and eggs are deposited on the inside of the cocoon or on the surface of the larva. Over one thousand eggs have been counted in one early-spun cocoon resulting from the oviposition of several females, while the greatest number of cocoons of *S. extrematis* in a single *Cecropia* cocoon was 172. As no starved larvae have been found, cannibalism is indicated. The average infestation of *Cecropia* cocoons with *S. extrematis* was found to be thirty-three. During oviposition, the host larva is thrust with the ovipositor and invariably dies within a few hours. The larvae of *S. extrematis* move about freely over the dead host larva at first feeding on cuticle, later burrowing down and drinking the body fluids. In cases of heavy parasitism all the host body is eaten except the few chitinized parts. In the Chicago area *S. extrematis* is double brooded, completing a cycle in about eighteen days.

Aenoplex smithii (Packard), the secondary ichneumonid parasite of this chain, appeared in about 13 per cent of the Cecropian cocoons which were infected with *S. extrematis*. Because its host larvae are available throughout the year (fig. 2), the number of broods of *A. smithii* appearing in a

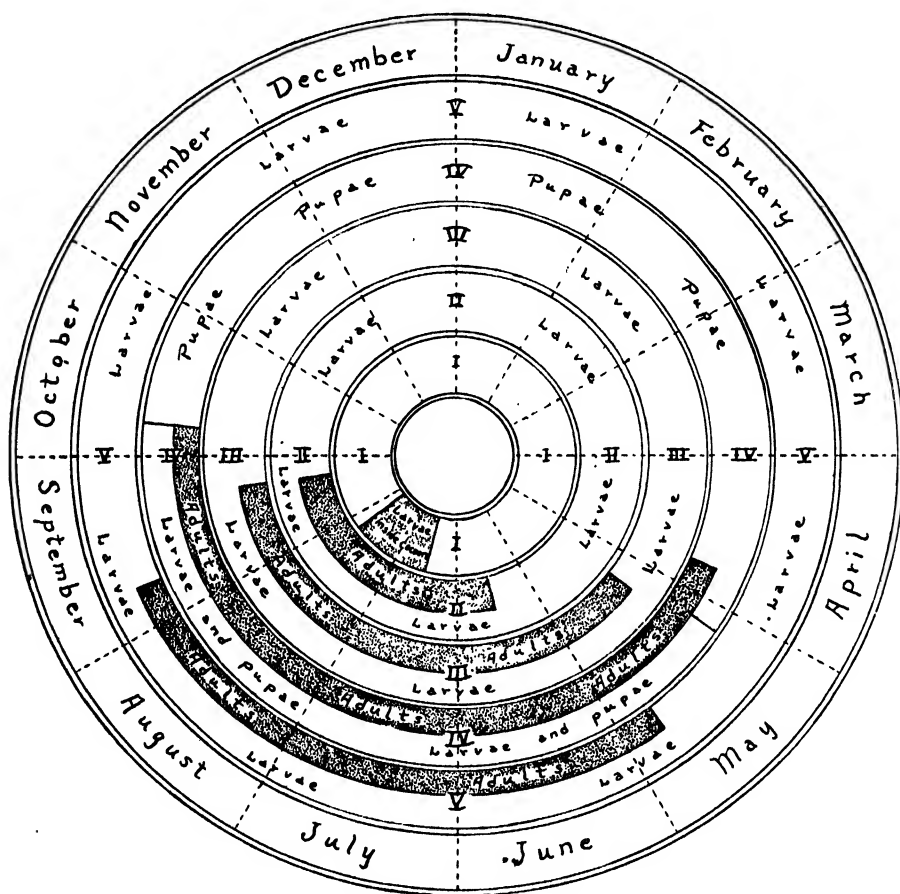


FIG. 2. Correlation of interrelated stages in the life-histories of members of the five-linked chain. I. *Samia cecropia* L. II. *Spilocryptus extrematis* Cres. III. *Aenoplex smithii* Pack. IV. *Dibrachys boucheanus* Ratz. V. *Pleurotropis tarsalis* Ash.

season is governed by the duration of the warm weather. Five successive groups of adults commonly appeared in a season in the area studied. The host larvae are located by careful palpation of the infected Cecropian cocoon with the antennae of the female. Due to the rather short ovipositor only those larvae cocooned in the periphery of the cavity inside the Cecropian cocoon can be reached. A single egg (rarely two) is laid inside the cocoon of each host larva. This larva is then thrust with the ovipositor and dies

within a few hours. The larva of *A. smithii* is very active, moving about freely over the dead host drinking at numerous punctures made by its mandibles. As in the case of *S. extrematis* the cycle of *A. smithii* required about eighteen days.

The omnivorous, cosmopolitan chalcid, *Dibrachys boucheanus* (Ratzeburg) appeared most frequently as a secondary parasite on *S. extrematis*, but because of the biological interest in its very frequent appearance as an accidental tertiary parasite of *A. smithii*, it is so listed here. Entrance to infected Cecropian cocoons is effected through holes previously made by woodpeckers, mice, or escaping ichneumonids, or if no holes are present, by crowding through the loose silk of the valve. Once inside, by palpation of the cocoons of *S. extrematis* with its antennae it determines the presence of a host larva and inserts its ovipositor, placing eggs on the surface of the larva. If a cocoon of *A. smithii* chances to be inside, its thin wall is also punctured and eggs deposited. An average of seven eggs were placed on *A. smithii* and twelve on *S. extrematis*. As many as fifty-three pupae have been found on the remains of one larva of *S. extrematis*. *D. boucheanus* is a very effective controlling factor. Each female may lay from 300 to 400 eggs and six broods were found in the field in a season. In the laboratory the writer reared nineteen generations of *D. boucheanus* in twelve months. Contrary to the report of Muesebeck and Dohanian ('27), the writer found that in the Chicago area *D. boucheanus* always hibernated as a straw-colored pupa.

The last place in this five-linked chain of insects was occupied by the small chalcid *Pleurotropis tarsalis* (Ashmead). According to the easy shifting of its host from the role of an obligatory secondary to that of an accidental tertiary, *P. tarsalis* naturally frequently occurred as either an obligatory tertiary or an accidental quaternary parasite. The larva of this chalcid is an internal feeder. The female, after gaining access to the Cecropian cocoon in the same manner as *D. boucheanus*, places a single egg (rarely two) just beneath the cuticle of the mature larva or freshly formed pupa. In this case the adult parasite does not kill the host, but this is accomplished later in the pupa case by the development of the parasite larva. From laboratory rearings and field observations in this area, *P. tarsalis* appears to complete at least three cycles during a summer. It invariably hibernates in the larval stage.

SUMMARY

Figure 2 pictures a brief summary of the fundamental facts in the life-histories of these insects, each species being considered as a unit, which are necessary for a correlation of the cycles of the species of this food chain. The figure is arranged to show the susceptible calendar period of each host in juxtaposition with the active or oviposition period of its parasite. This nicely balanced series in conjunction with the other regulatory factors of Cecropia in the Chicago area seems to have produced an equilibrium in the

abundance of the moth. The infestation of this moth is abnormally heavy, yet has apparently been of this degree for some time. As expressed in the words of an interrogated "native" who had grown up in the area, the cocoons had "always been just that thick." A reasonable balance does appear to have been reached in the infestation by this moth so that, in recent years at least, *Cecropia* has neither increased nor decreased.

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MICROFOSSIL SUCCESSION IN A BOG IN NORTHERN WISCONSIN *

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A stratigraphical and statistical study of the microfossils in the marginal mat of a small bog lake in Vilas County, Wisconsin, was undertaken in an attempt to determine the plant succession of the region and to test a new method for determining the vertical extent of limnic and subaerial peat in a bog.

The deposit in which these observations were made is known to the Wisconsin Geological and Natural History Survey as the Forestry Bog Lake, and is located near its Limnological Laboratory in Section 8, Township 41 North, Range 7 East.

The depression in which the lakelet is located was formed by the melting of a buried ice mass in the pitted outwash plain of the Early Mankato Ice (Fourth Wisconsin). The soils surrounding the depression are predominantly sandy, but also contain lenses of gravel.

The area of the lake, which is in the center of the bog, is 993 square meters. Its maximum depth is 2 meters. The original area and depth were much greater.

Very early in the history of the Forestry Bog Lake there was a connection on the southern side with Trout Lake. How long this persisted is impossible to state, but the condition of the topography suggests that it was very brief and may have been connected only during the melting of the glacial ice at this point.

The lakelet (fig. 1) is in the late stage of old age, as is shown by the presence of organic soils, shallow water and an irregular shoreline of peat (Wilson, '35).

According to Fassett ('30), the plants growing upon the peat bog are *Sphagnum* sp., *Sarracenia purpurea*, *Monotropa uniflora*, *Smilacina trifolia*, *Chiogenes hispidula*, *Rhynchospora alba*, *Picea mariana* bearing *Arceuthobium pusillum*, *Eriophorum virginicum*, *Larix laricina*, *Carex oligosperma*, *C. pauciflora*, *C. trisperma*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Gaultheria procumbens*, *Vaccinium oxycoccos*, *Menyanthes trifoliata*, *Kalmia poli-*

*From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey and Coe College. Report No. 64. The publication of the illustrations in this article was provided for by funds other than those of the Ecological Society of America.

folia, and *Andromeda glaucophylla*. Two shrubs, which also occur on the bog, but near its periphery are *Alnus incana* and *Betula pumila*, var. *glandulifera*. These were not listed by Fassett.



FIG. 1. The Forestry Bog Lake.

The plants occurring in the waters of the lake are *Utricularia vulgaris*, var. *americana*, the yellow pond lilies, *Nymphaeozanthus variegatus*, and *N. microphyllus*, and *Brasenia schreberi*.

The peat for this study was obtained by the use of a Davis peat borer. The material was taken half way between the edge of the mat and the original shoreline on the west side of the lakelet. With the available equipment it was impossible to recover sediments from the deepest part of the deposit. It is therefore assumed that the earliest sediments of the lake were not obtained.

The samples were placed in vials and preserved in a 30 per cent solution of alcohol. In the laboratory about 16 cc. of the contents of each bottle was placed in a beaker containing 100 cc. of distilled water. This mixture was allowed to come to the boiling point in order to better separate the peat, and it was then strained through a coarse and a fine copper sieve twice. Four drops of saffron were added to the strained sediment, and then it was centrifuged. The clear liquid was poured off and to the concentrated sediment was added 15 cc. of glycerine jelly. Following this procedure the material was allowed to stand in the desiccator for from 24 to 48 hours. Next the container and jelly were heated in hot water until the latter was fluid. It was then stirred, and just enough solution was placed on a microscopic slide to float a No. 1 cover glass. Five slides were made of the material from each of the eight levels (table I).

Fifty spores or pollen grains were counted on each of four slides for every level by means of a mechanical stage. The fifth slide was for use in case there were not 50 microfossils on each of the other four slides. There were thus 200 microfossils counted for each of the eight levels. These were tabulated and the percentages taken for the different levels.

TABLE I. *Percentage of microfossils in the Forestry Bog*

Species	Depth in meters							
	5	4.5	3.5	2.5	2	1	.5	Surface
<i>Sphagnum</i>5	.5	1.5	3.0	1.5	3.5	.0	6.5
<i>Lycopodium annotinum</i> and <i>L. clavatum</i>	1.5	.0	1.5	.0	.0	.5	1.0	.5
<i>Pinus banksiana</i>	22.5	40.5	62.0	37.0	29.0	44.0	39.0	13.0
<i>P. resinosa</i> and <i>P. strobus</i> ...	61.5	53.0	31.5	49.5	46.5	42.0	34.5	14.0
<i>Picea</i>	9.5	3.5	.5	8.0	18.5	3.5	8.5	5.0
<i>Abies</i>5	.5	.0	.5	1.5	.0	.0	.0
<i>Betula</i>	1.0	.5	1.0	2.0	3.0	5.5	4.0	27.5
<i>Alnus</i>0	.0	.0	.0	.0	.0	.5	1.0
<i>Nymphozanthus</i>0	1.0	3.0	.0	.0	.0	.0	.0
<i>Acer</i>	1.5	.0	.0	.0	.0	.0	.5	5.0
<i>Tilia</i>5	.0	.0	.0	.0	.0	.5	1.5
Ericaceae.....	.0	.0	.0	.0	.0	.5	1.0	1.0
Compositae.....	1.0	.5	.0	.0	.0	.5	.5	25.0

The water lily trichomes and the barbed and plain sponge spicules were counted in another manner. By means of the mechanical stage the number of trichomes or sponge spicules per square centimeter was determined. The results for four slides were averaged for each level, and a graph was made showing a comparison of these (fig. 2).

The sponge spicules are probably of *Spongilla lacustris* and *S. fragilis*. It will be noted that there is an abundance of both barbed and plain sponge spicules at the 5 meter level. This abundance decreases rapidly and there are comparatively few spicules in the 4.5 meter and 3.5 meter levels. This decrease might have been due to the water becoming softer and somewhat toxic so that it was unsuitable for the growth of sponges. The rapid increase in the number of water lily trichomes up to the 3.5 meter level, and then the total absence of these in the following level may in part discredit the theory that the decrease of the sponges was due to the toxicity of the water. It is possible that this disappearance of spicules and trichomes would be better correlated with the development of the organic mat which surrounds the lake. As this mat developed and grew outward into the lake and covered the limnic peat, it also pushed the aquatic life toward the center of the lake. Limnic peat contains such fossils as water lily pollen, internal trichomes of water lilies, and sponge spicules, while peat formed above water contains none of these.

Therefore by a study of the vertical distribution of such fossils it is possible to separate peat of limnic and subaerial origin.

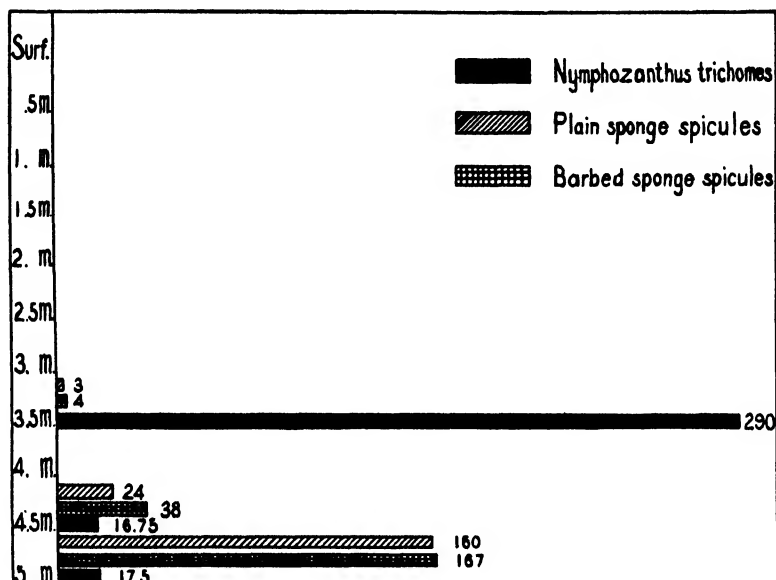


FIG. 2. A numerical comparison of the lily trichomes and sponge spicules in the limnic peat of the Forestry Bog. The counts represent an average taken from one square centimeter of prepared peat material on four different slides for each level.

Very little *Sphagnum* is found in the lower levels from which samples were taken, but the amount increases toward the surface. This increase would indicate that a *Sphagnum* moss mat was forming about the lake. Other plants that would grow upon such a mat are *Betula pumila*, var. *glandulifera*, *Picea*, and several species of *Ericaceae*. Their relative increase in abundance as fossils might indicate that this was actually taking place, and might be correlated with the change in composition of the peat.

If the basal sediments from the center of the lake had been studied, they would probably have been composed of almost 100 per cent *Picea* pollen. This is indicated by other research in the region. At the 2.5 meter level the spruce fossils increase in abundance. This, also, may be correlated with the appearance of the organic mat around the lake, as shown by the disappearance of aquatic fossils.

Picea, as well as *Pinus banksiana*, *P. resinosa* and *P. strobus*, is much more abundant in the lower levels and decreases toward the top, apparently due to the greater relative abundance of angiosperms, and also due at the surface to deforestation by lumbering operations and forest fires (fig. 3).

The *Betula* fossils include both the upland and bog species, the latter spe-

cies probably constituting the larger percentage of these fossils. *Alnus*, *Acer* and *Tilia* fossils follow the curve of the birch.

A small percentage of Compositae pollen is found in the 5 meter and the 4.5 meter levels. At this stage of the lake development the shores were

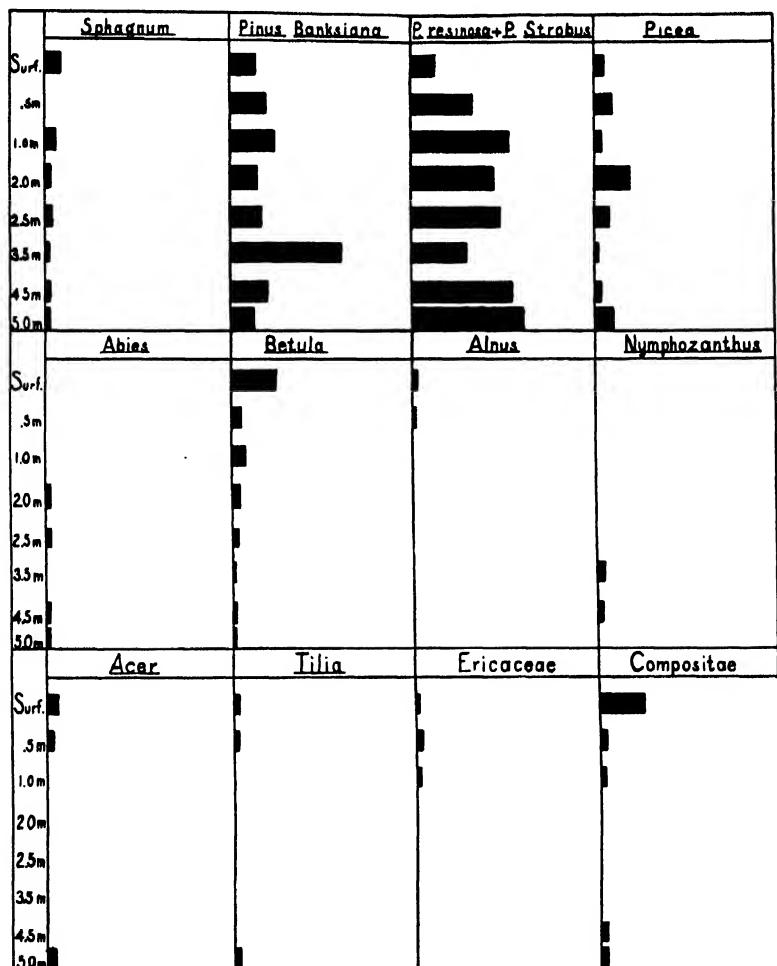


FIG. 3. A comparison of the microfossil abundance in the Forestry Bog. The total width of each column represents 100 per cent. For exact per cent, see table I.

probably sandy. When the *Sphagnum* mat developed, the composites were excluded from the edge until the mat had matured. The rapid rise in the percentage at the surface may represent an invasion into the region of the prairie flora after the deforestation of the trees.

SUMMARY

The use of sponge spicules and water lily trichomes for determining the vertical distribution of limnic and subaerial peat in bog deposits was found to be an accurate method.

The microfossils indicate that the regional flora was dominated early in its history by a coniferous element, and that this was gradually replaced by angiosperms.

The authors are indebted to the Wisconsin Geological and Natural History Survey for the peat samples used in this investigation.

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COMPARATIVE STUDY OF BOGS ON CARY AND TAZEWELL DRIFT IN ILLINOIS¹

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An important matter which some writers fail to take cognizance of in the correlation of widely separated peat deposits from a pollen analysis standpoint, is that the materials upon which the bogs lie often vary considerably in age. In 1933 the writer published the results of the pollen analyses of seven Late Wisconsin bogs found within the confines of Lake County, Illinois. The term, Late Wisconsin, formerly of common usage among glaciologists, is now replaced by Cary and likewise the term Tazewell is synonymous with what was formerly known as Early Wisconsin. During the Cary and Tazewell substages of the Wisconsin, many terminal moraines were formed in the northern half of Illinois as shown in figure 1. The terminal moraines of the Tazewell substage arranged in a chronological order from the oldest to the youngest are as follows: Shelbyville, Cerro Gordo (Inner and Outer), Leroy, Champaign, Bloomington, Normal, Cropsey (Inner, Middle, and Outer), Farm Ridge, Chatsworth, and Marseilles.

The Bloomington is the most pronounced moraine of the series and it served as the bank of an extensive lake known as Lake Illinois which persisted from the close of the Bloomington stage to Marseilles times. Subsequent to the construction of the Bloomington moraine, the younger moraines were formed by retreats and advances of the ice sheet, the direction of the moraines (figure 1) indicating that the ice did not always follow the same course.

The terminal moraines of the Cary substage arranged in the same chronological order as the ones above are as follows: Minooka, Rockdale, Manhattan, West Chicago, Valparaiso, Tinley, and Lake Border—Inner, Middle, and Outer.

The bogs described by the writer in 1933 all lie on Valparaiso drift which is, according to Leighton, probably ten thousand years younger than the Bloomington. During the past year pollen analyses were made of nine bogs connected with the Bloomington, Normal, Cropsey, and Chatsworth moraines.

The numerous sources of error involved in pollen statistics, such as pollen production, wind transportation, favorableness of bogs for receiving and preserving the pollen, variability in rate of pollen decay, flotation, and

¹ The publication of excess diagrams in this article has been made possible by funds other than those of the Ecological Society of America.

time of flowering have already been discussed by various writers such as Erdtman, '31; Fuller, '35; Sears, '30; and Voss, '34. Another factor which should be added to the list is the biotic. In one of the bogs included in this paper, the writer encountered a layer of shell marl seven and one-half meters

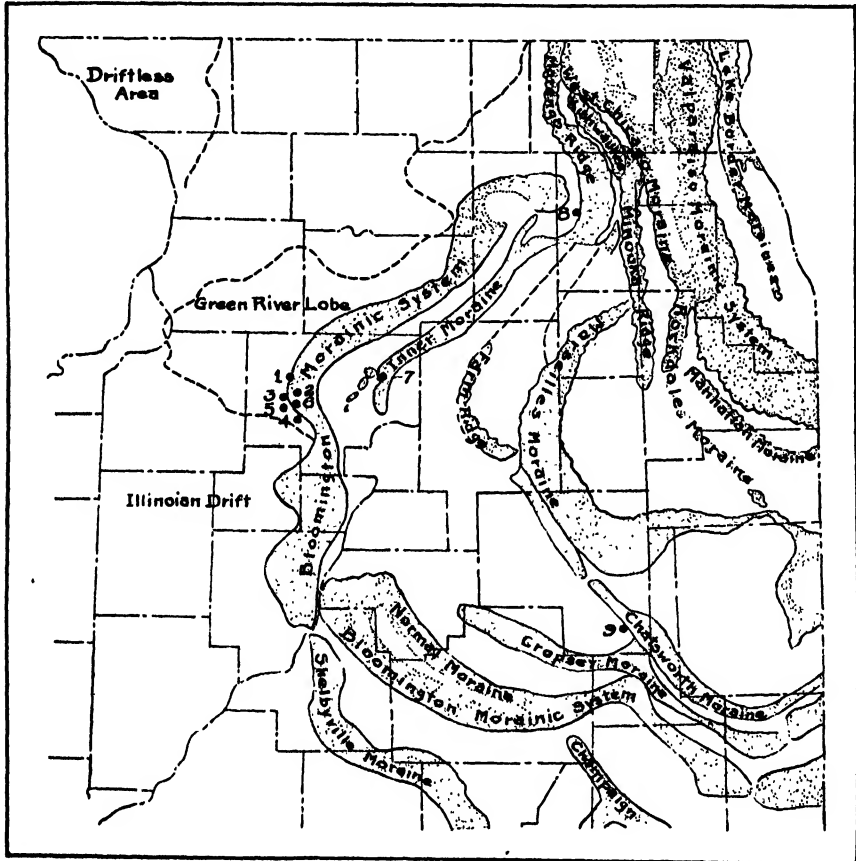


FIG. 1. Map of terminal moraines of the Wisconsin ice sheet showing the locality of the bogs (After Leighton). 1, North Manlius; 2, South Manlius; 3, Langley; 4, Buda; 5, North Sheffield; 6, Canal; 7, Arlington; and 8, Lily Lake bog.

thick. The mollusks comprising it were all aquatic forms and gradually increased from a few specimens at the bottom to many at the top of the layer. Near the middle of the marl layer, the pollen frequency decreased with the increase in the number of snails and finally the pollen frequency became so low, that the counts were unreliable for pollen statistical use. Submerged vegetation supplied the food for the aquatic mollusks and, not only were the plants eaten, but also the foreign organic materials such as some of the pollen grains which became attached to the plants.

The interpretation of pollen diagrams, as Fuller ('35) has pointed out, represents a general picture of the vegetation over a wide area since the source of the pollen found in peat may range from the bog itself, to points over five miles distant from the bog. Regarding climatic changes they can, as Aario ('32) has indicated, be best interpreted from pollen diagrams not so much by the increase or decrease of certain genera as by the appearance or disappearance of the genera during the development of the bog.

LOCATION AND DESCRIPTION OF BOGS

Nine deposits which, during the past three decades, have been drained, supplied the materials for the present study. The bogs, unlike those of Lake County, Illinois, contained no remains of sphagnum. The locations are as follows (fig. 1).

The North Manlius bog is situated one mile north of the town of Manlius in Sections 2 and 11, Township 17 N, Range 7 E, Bureau County, Illinois. It is two miles in length and where the Chicago and Northwestern Railroad crosses the deposit, it is one mile in width. A portion of the bog is now under cultivation.

The South Manlius deposit is located 3 miles south of Manlius, Bureau County, Illinois, in Section 34, Township 17 N, Range 7 E. It covers an area of about 80 acres. Attempts have been made to cultivate it but without success. During dry periods the loose dust-like peat is picked up by winds and deposited in the form of dunes along the nearby fences.

The Langley bog is three quarters of a mile south of Langley in Section 21, Township 16 N, Range 7 E, Bureau County, Illinois. It occupies an area of about 80 acres and the vegetation consists principally of grasses. The Chicago and Northwestern Railroad tracks cross it in a north-south direction.

The Buda deposit is found in Sections 27 and 28, Township 16 N, Range 7 E, one and one-half miles north of Buda, Bureau County, Illinois. The deposit has been under cultivation for a number of years.

The North Sheffield bog covers portions of Sections 1, 2, 11, 12, Township 16 N, Range 6 E, Bureau County, Illinois, and occupies an area of approximately 180 acres. It is now used for agricultural purposes.

The Canal bog, so called since the Illinois-Mississippi Canal passes through it in an east-west direction, is over a mile in length and three-fourths of a mile in width. It can be found in Section 11, Township 16 N, Range 7 E, Bureau County, Illinois. The canal furnishes excellent drainage and the former swamp is now under cultivation.

The Arlington bog is a peat-filled lake in Section 7, Township 17 N, Range 11 E, Bureau County, Illinois, and comprises an area of sixty acres.

Lily Lake is a long, narrow bog running east and west in Sections 19 and 20, Township 40 N, Range 7 E, Kane County, Illinois. Most of the bog is now under cultivation,

The Chatsworth deposit is in Section 32, Township 26 N, Range 8 E, Livingston County, Illinois, five and one-half miles southeast of the city of Chatsworth. It consists of a seven and one-half meter layer of marly peat below which there is a thick layer of muck and above, a meter of well decomposed peat. The marl is now being removed for commercial purposes.

PRESENTATION OF RESULTS

Stratigraphic evidence shows that the time interval between the formation of the Bloomington and Normal moraines in Bureau County was extremely short. The North Manlius bog is either associated with the retreat of the Bloomington or the advance of the Normal ice. The peat deposit is not very thick and if the peat accumulated as rapidly as that on the Valparaiso drift, the age of which is estimated to be not over 25,000 years, the

TABLE I. Percentages of fossil pollen found in the North Manlius bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Acer</i>	<i>Alnus</i>	<i>Betula</i>	<i>Carya</i>	<i>Cellis</i>	<i>Carpinus</i>	<i>Juglans</i>	<i>Quercus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
1.00			9.8	1.6		4.9	4.9				67.0	4.9	4.9	1.6
1.50			11.9			1.8	9.1				53.0	7.3	7.3	7.3
1.72		.7	4.5				12.0		.7	.9	51.0	3.0	7.0	15.0
2.00	1.3	25.0	39.0	1.3	1.3	11.2		3.0			13.8	2.6	1.9	2.6
2.22	3.6	21.6	23.5			6.3	.9				41.5			.9
2.50	3.9	41.0	27.0			2.3	2.3				20.5	1.5		.7
2.72	13.8	70.0	14.8											.9
3.00	16.6	56.0	25.8								1.6			
3.50	8.9	46.5	37.7								6.6			

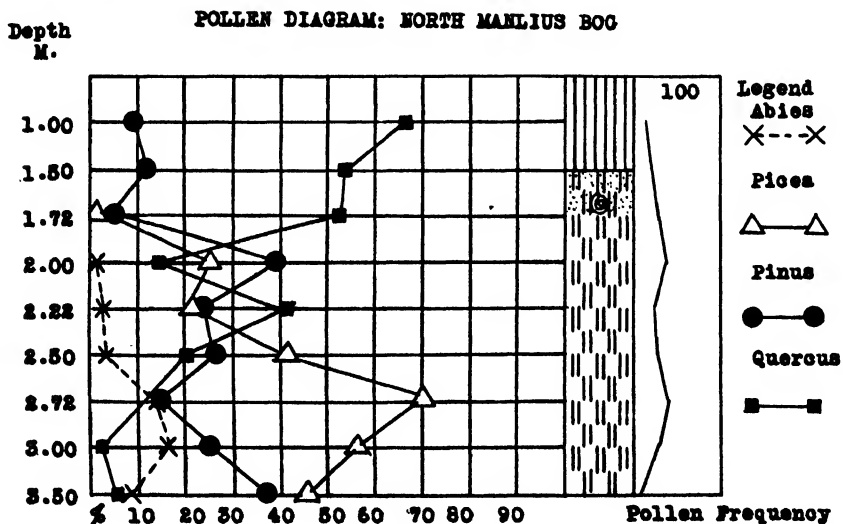


FIG. 2. Pollen diagram of the North Manlius bog.

North Manlius depression could have been, if conditions had been favorable, completely filled long before the advance of the Valparaiso ice sheet. *Picea* and *Pinus* were the first dominant pollen in the history of the bog, *Abies* and *Quercus* being present in lesser quantity (table I, fig. 2). *Pinus* decreased

TABLE II. Percentages of fossil pollen found in the North Sheffield bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Carya</i>	<i>Celtis</i>	<i>Ostrya</i>	<i>Juglans</i>	<i>Populus</i>	<i>Quercus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
1.00			7.4		11.1	3.7	3.7		3.7	63.0	7.4		
1.50			8.7	1.4	2.9					81.0	1.4	1.4	2.9
2.00			7.1	5.5	11.0					65.4		3.1	7.9
2.22		1.3	26.2	16.8	1.3					45.0		.6	8.7
2.50		4.4	44.7	8.0	.8	.8		1.7		33.0			6.2
2.72		13.6	48.0	6.4	.8	1.6				28.0			1.6
3.00		45.5	24.6	6.7	.7	2.2				19.4			.7
3.50	2.4	80.6	12.9	.8						3.2			
3.72	3.0	83.0	13.1							.7			
3.86	5.1	82.6	11.2							.8			
4.00	7.5	77.0	15.1										
4.50		82.7	16.4	.9									
5.00		81.2	16.3							2.0			
5.22		83.8	10.8							5.4			
5.50	7.4	50.6	32.1	1.2						7.4			1.2

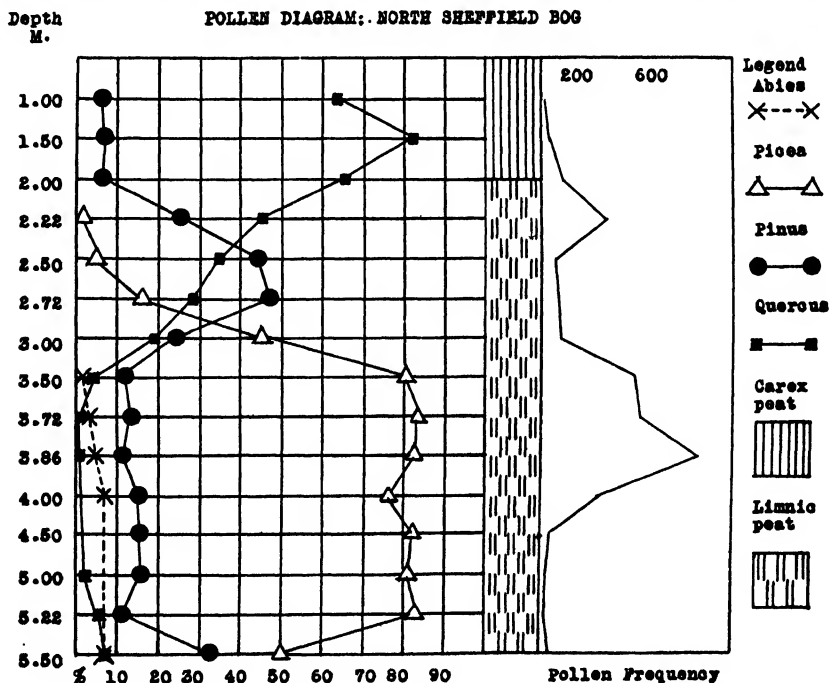


FIG. 3. Pollen diagram of the North Sheffield bog.

and *Picea* advanced and remained dominant until the 2.72 meter level, following which it gradually diminished and disappeared above the 1.72 meter mark. At 2 meters *Pinus* forged ahead of *Quercus*, the latter having been dominant over the former at the 2.22 m. mark. Above 2 meters, *Quercus* again increased and remained the most abundant pollen. Both *Betula* and *Carya* appeared at 2.5 meters and remained in moderate quantities up to the youngest pollen-bearing layer. The pollen frequency of the upper layers due to drainage and oxidation unfortunately was so low that the percentages were not trustworthy. This is also true of other deposits described in this paper.

The North Sheffield deposit is connected with the Bloomington moraine. Its pollen curves are strikingly similar to those of the North Manlius bog; *Abies* and *Picea* respectively disappearing near the middle and top. Also a *Pinus* maximum occurs above the middle. At the 1 meter level there is a decrease in the quantity of *Quercus* (table II, fig. 3).

The Langley bog (table III, fig. 4) like that at North Manlius may either be associated with the retreat of the Bloomington or the advance of the Normal ice. The chief differences in the two pollen diagrams are that

TABLE III. Percentages of fossil pollen found in the Langley bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Alnus</i>	<i>Betula</i>	<i>Carya</i>	<i>Celtis</i>	<i>Quercus</i>	<i>Salix</i>	<i>Ulmus</i>
1.00		15.9	54.2	1.0	3.2	2.1	1.0	20.2		2.1
1.50		18.4	35.0		5.2		3.5	30.7	4.4	2.6
2.00	2.0	28.0	41.2	1.0	4.1	1.0		15.4	4.1	3.1
2.22	.6	20.8	43.5		4.8	2.8		25.0	.6	1.3
2.50	3.9	44.5	37.7		2.6			9.9	.6	.6
3.00	3.0	68.5	23.7					4.6		
3.50	7.5	52.5	30.0		5.0			5.0		

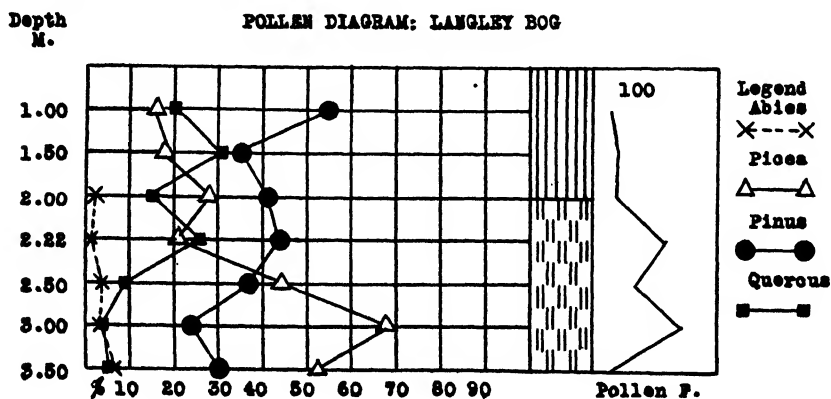


FIG. 4. Pollen diagram of the Langley bog.

Picea was present in the layers nearer the surface and *Pinus* pollen was dominant in the youngest pollen-bearing layers of the Langley peat. Also a decrease of *Quercus* similar to that already mentioned in regard to the North Sheffield bog was noted in the youngest layers.

The Canal deposit is found in the Normal moraine. Its pollen curves are in general similar to those of the Langley, *Pinus* again being the outstanding pollen in the top layers (table IV, fig. 5).

TABLE IV. Percentages of fossil pollen found in the Canal bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Acer</i>	<i>Betula</i>	<i>Carya</i>	<i>Carpinus</i>	<i>Ostrya</i>	<i>Juglans</i>	<i>Populus</i>	<i>Quercus</i>	<i>Salix</i>	<i>Ulmus</i>
1.00		5.3	60.0	1.0	4.3	2.1					23.6	1.0	2.1
1.22		2.6	34.4		3.5	4.4					47.8	.8	4.4
1.50		4.3	45.6		5.1	.8	.8	.8	.8	.8	31.8	6.0	3.4
1.72		11.2	65.5		2.5		.8				18.1		1.7
2.00		20.3	62.7		3.5						8.8	3.5	.8
2.22		33.6	62.5								2.8	.9	
2.50	2.5	55.0	39.6								2.5		

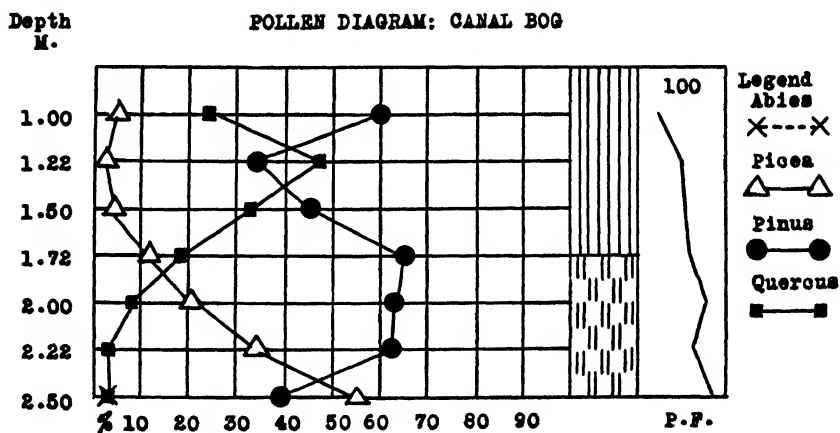


FIG. 5. Pollen diagram of the Canal bog.

The South Manlius and Buda bogs are both post-Normal in age, the chief difference in their pollen diagrams being the fact that *Quercus* in the latter continued to decrease after reaching its maximum at the 4 meter level (tables V, VI, figs. 6, 7).

The Arlington depression is in the Arlington moraine which at this locality is considered to be a part of the Inner Cropsey. There might be, according to Leighton, a time difference of a thousand or two thousand years between the building of the Bloomington and Arlington moraines. *Abies* and *Picea*

TABLE V. Percentages of fossil pollen found in the South Manlius bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Carya</i>	<i>Cellis</i>	<i>Jug- lans</i>	<i>Quer- cus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
1.00			4.4	.8	3.5	1.7	2.6	82.5		.8	3.5
1.72			6.6	1.3	9.2		3.9	74.0			5.2
2.00			6.9	.9	9.1	5.5	2.7	61.5		.9	12.8
2.22			12.8	1.5	10.6	1.5	3.8	53.0		.7	15.9
2.50			8.5	6.6	7.3	2.4	4.8	50.0		3.0	16.3
2.72		1.1	14.3	13.1	3.4			49.0			18.8
3.00	3.7	39.1	16.1	13.7	4.9			10.6	.6		11.4
3.50	2.8	72.5	14.8	2.8	.7			5.6	.7		
3.72		91.0	7.6					.7			
3.86		87.5	5.1	2.0		3.0		2.0			
4.00	2.2	86.0	2.2	2.2		2.2		3.3	1.1		

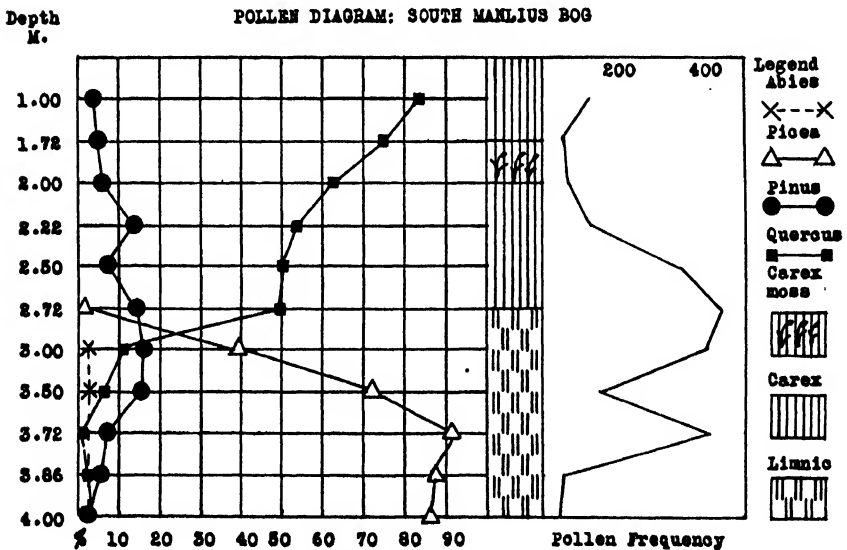


FIG. 6. Pollen diagram of the South Manlius bog.

TABLE VI. Percentages of fossil pollen found in the Buda bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Carya</i>	<i>Car- pinus</i>	<i>Jug- lans</i>	<i>Quer- cus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
3.22			2.1	1.0	14.0	2.1	4.3	47.3		6.4	22.6
3.50			7.3		5.2	1.1	4.2	54.7		3.1	24.2
3.72			3.6	3.6	2.4		1.2	56.5			32.4
4.00			3.0	4.0	1.0	4.0		67.2			20.4
4.22		4.0	4.0	10.0	2.0	2.0	2.0	56.0		1.0	19.0
4.50		12.5	32.5	8.7	2.5	1.2		31.3		1.2	10.0
4.72		14.8	17.3	8.6	3.7			39.5			16.0
5.00	1.0	19.6	24.0	1.0	1.0	1.0		43.5	2.1		6.4
5.50	9.1	68.2	16.7		1.5			4.5			
6.00	12.3	50.8	17.6	5.2	1.7			10.5	1.7		

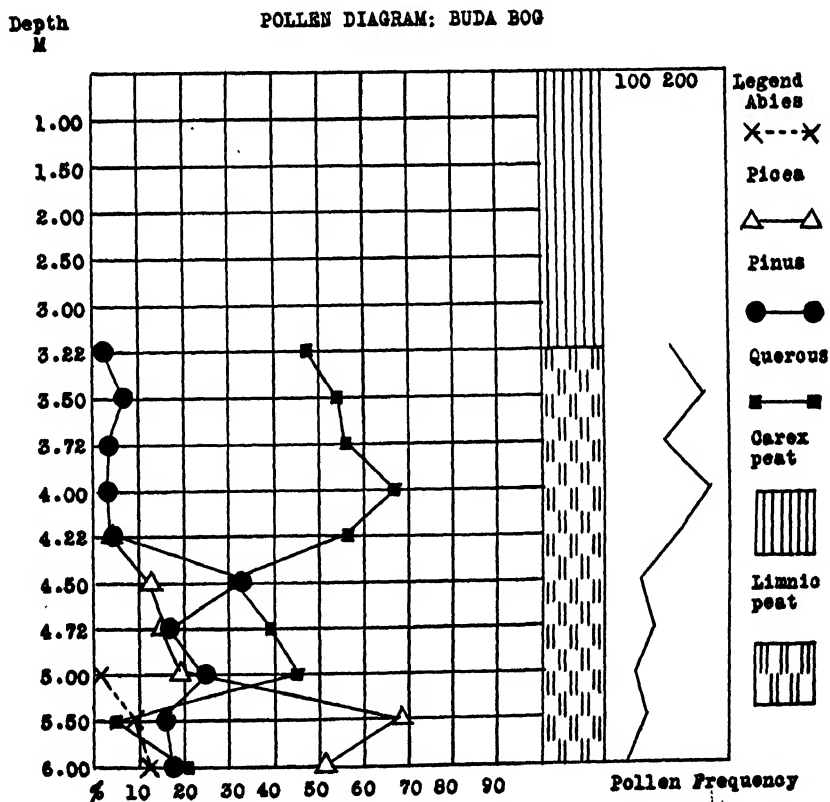


FIG. 7. Pollen diagram of the Buda bog.

disappeared early while *Quercus* rapidly increased and remained dominant during most of the postglacial period (table VII, fig. 8).

TABLE VII. Percentages of fossil pollen found in the Arlington bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Acer</i>	<i>Betula</i>	<i>Carya</i>	<i>Ostrya</i>	<i>Juglans</i>	<i>Quercus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
2.00			4.0			9.5			81.0			4.0
2.50			6.1	1.3	.6	12.2		4.1	66.0		3.4	6.1
3.00			2.4	.8	1.6	10.6	.8	3.2	72.0		.8	7.3
3.22			2.7	.9	.9	6.5		2.7	78.0		3.7	4.6
3.50			7.5			6.0		1.5	76.5		3.7	4.5
4.00			12.2	.6	2.7	5.4	1.3	.6	65.0	2.7	4.0	5.4
4.22			11.5			11.5		9.5	68.5			
4.36			6.4		6.4	3.2			77.5	3.2	3.2	
4.50			6.2		1.3	6.2		1.3	75.0		2.0	7.6
5.00			5.6		2.4	.8	.8	1.6	83.0		2.4	3.2
5.50		2.5	8.3		1.9	7.0		2.5	66.0		1.2	9.5
6.00	1.3	29.5	5.9		5.2	3.9		1.9	51.0	.6		
6.50	9.2	65.0	4.2		5.6	4.2			8.5	2.1		.7

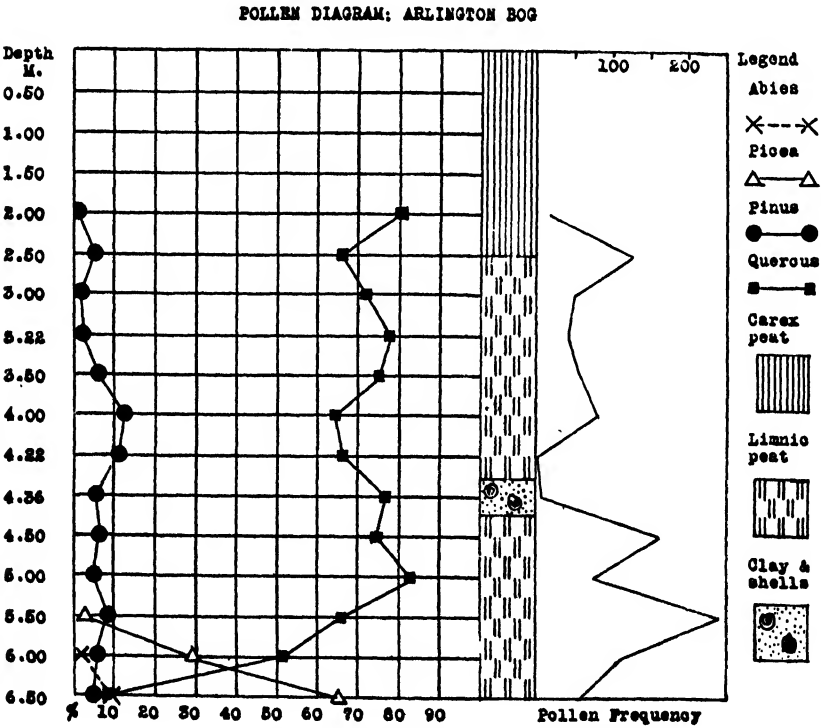


FIG. 8. Pollen diagram of the Arlington bog.

The Lily Lake peat is in the Elburn moraine which is believed to be the equivalent of the Cropsey. Its pollen diagram is practically identical with the Arlington (table VIII, fig. 9).

TABLE VIII. Percentages of fossil pollen found in the Lily Lake bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Carya</i>	<i>Carpinus</i>	<i>Ostrya</i>	* <i>Juglans</i>	<i>Quercus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
4.00			7.4	11.0		1.2		1.2	65.2		2.4	11.1
4.22			11.4	5.0	6.3	1.2		1.2	59.5		5.0	10.1
4.50			8.3		11.1	1.3		1.3	69.5		4.1	4.1
4.72			8.3	1.1	5.9	1.1	1.1	2.3	66.6			13.1
5.00			5.0	1.2	11.2	1.2	1.2		57.5	1.2	5.0	16.3
5.22		1.6	8.3	3.3	6.6		1.6		68.5		3.3	6.6
5.50		10.5	22.1	15.8					38.0	2.1	1.0	10.5
6.00	8.3	56.2	29.2	4.1					2.0			

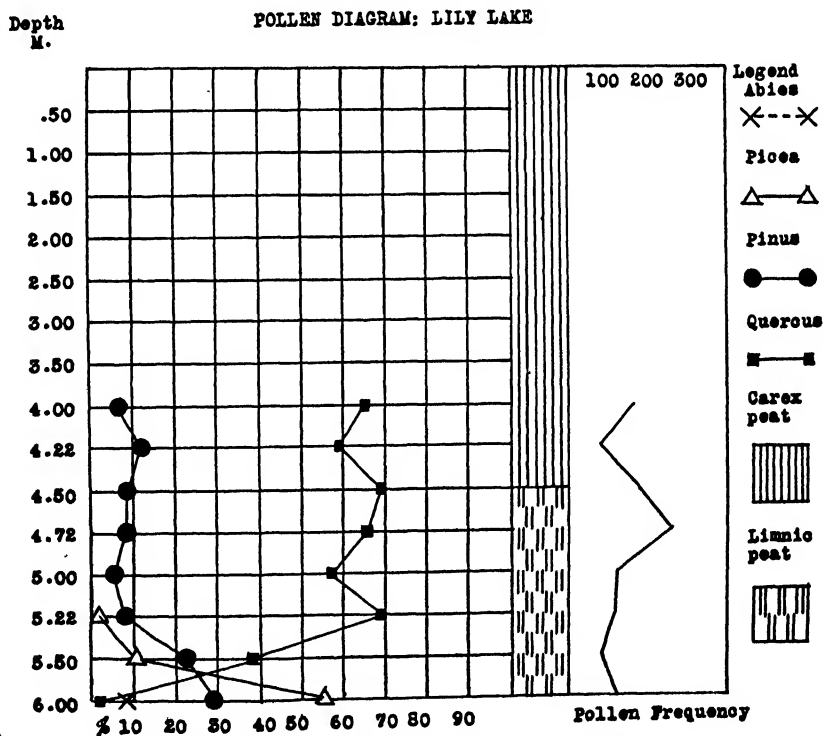


FIG. 9. Pollen diagram of the Lily Lake bog.

The Chatsworth bog, which is the deepest and youngest of the Tazewell group, is located just outside of the Chatsworth moraine. A layer of muck

TABLE IX. Percentages of fossil pollen found in the Chatsworth bog

Depth M.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Carya</i>	<i>Celtis</i>	<i>Car-</i> <i>pinus</i>	<i>Ostrya</i>	<i>Jug-</i> <i>lans</i>	<i>Pop-</i> <i>ulus</i>	<i>Quer-</i> <i>cus</i>	<i>Salix</i>	<i>Tilia</i>	<i>Ulmus</i>
6.50			6.8		10.1						76.2		1.7	5.0
6.72			5.8	1.4	11.6						75.4		2.9	2.9
7.00			4.8	1.6	11.3						74.0		3.2	4.8
7.22			4.3		7.2						80.0		2.9	5.8
7.50			1.2	1.2	6.4	1.2					84.5		2.5	2.5
8.00					12.1			1.1		1.5	70.0	3.0	1.5	10.6
8.50			10.0	3.7	2.5		1.2	2.5			68.8		2.5	8.7
9.00		3.1	10.9	4.7	3.1			3.1			65.7	1.5	1.5	6.2
9.50														
9.72														
10.00		15.8			5.2				5.2		63.0			11.0
10.22														
10.50														
10.72			5.2	15.8	11.0	3.5	1.7				58.0			5.2
11.00			28.7	47.5	4.9						15.8	.9	.9	
11.22	1.8		63.0	27.4	1.8						5.5			
11.50	2.0		45.8	48.0	2.0						2.0			

Depth
M.

POLLEN DIAGRAM: CHATSWORTH BOG

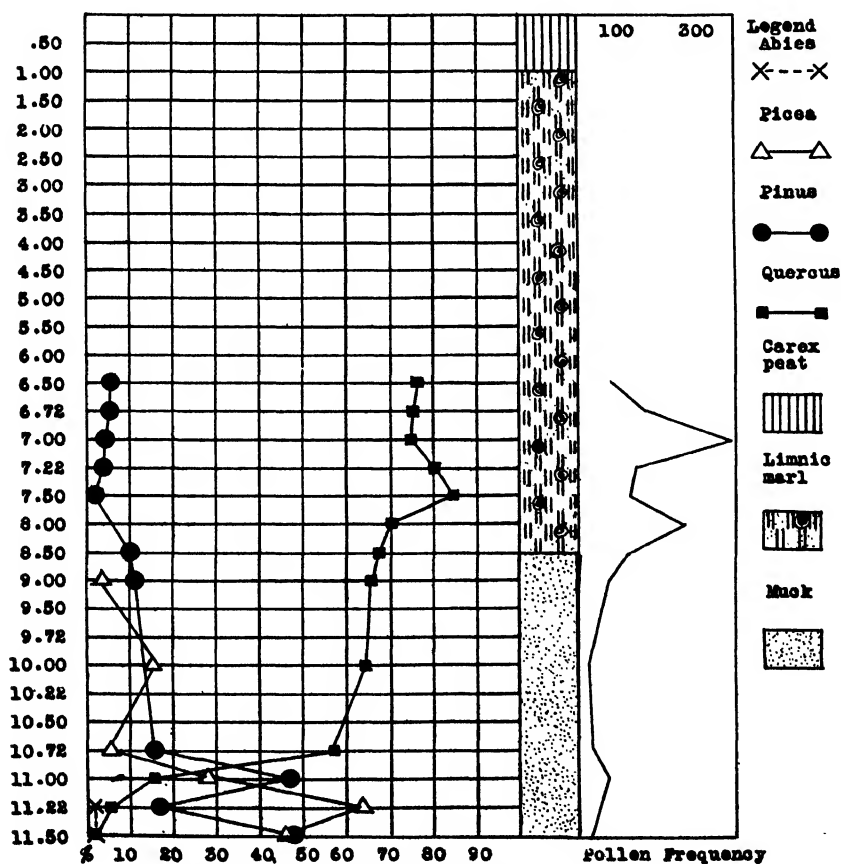


FIG. 10. Pollen diagram of the Chatsworth bog.

3 meters in thickness having a very low pollen frequency was found on the bottom. Above the muck, a 7.5 meter layer of marly-peat occurred upon which rested a meter of well-decomposed *Carex* peat. Between the 9 and 10.7 meter levels the pollen frequencies of the tree pollen were generally so low that they were not included in the pollen diagram (table IX, fig. 10). In this stratum *Ambrosia* pollen was exceedingly abundant. It would be unwise to assume that the climate during this period was drier than the preceding when *Picea* and *Pinus* reached their maximum. Also it would be foolish to surmise that the territory in the vicinity of the bog was practically treeless if the character of the pollen-receiving materials in the depression during that period are taken into account. A picture of the Chatsworth depression at that time would probably be that of a typical temporary pond which contained water in the early spring and was dry perhaps before the first of June. The lack of tree pollen could have easily been due to decomposition as a result of the lowering of the water table during the summer months. Although very little data are available regarding the resistance of various pollen to decay, it is possible that *Ambrosia* pollen is more durable than the tree pollen found at the bottom of and above the muck layer. The dearth of tree pollen at the above mentioned levels, no doubt, was due to local conditions since no layers of similar nature are found in the pollen records of the older Tazewell bogs.

TABLE X. *Mollusca from marl deposits in the Chatsworth bog*

Depth in meters	1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5
<i>Valvata tricarinata</i>	a	a	a	a	a	a	a	a	a	a	c	i	r		r	r
<i>Amnicola leightoni</i>	a	a	a	a	a	a	a	a	a	c	c	r	r	r	r	r
<i>Amnicola gelida</i>	a	a	a	a	a	a	a	a	a	c	a	r		r	r	r
<i>A. walkeri precursor</i>	c	c	c	r	c	r	c		r	c	c	r	r	r	r	r
<i>Physa</i> sp.	a	a	a	c	a	c	a	c	a	a	c	r		r	r	r
<i>H. anceps striatum</i>	r	c	c	c	c	r	r	c	c	c	c	r			r	r
<i>M. exacuous megas</i>	c	r	c	r	c		c	r	c	c	r	r				
<i>Gyraulus altissimus</i>	c	c	c	c	c	c	c	c	c	c	c	r	r		r	r
<i>Gyraulus deflectus</i>	c	c	r			r		r								
<i>Ferrissia fusca</i>		r														
<i>Pisidium</i> sp.	c	r														
Number of species	10	11	10	7	10	8	9	8	9	9	8	7	3	4	6	6

a. abundant. c. common. i. infrequent. r. rare.

Table X lists the mollusca identified by Prof. F. C. Baker from the marly peat above the muck. There was a gradual increase in the number of species from the bottom to the top and the following extinct forms were found: *Amnicola leightoni* F. C. Baker, *Amnicola gelida* F. C. Baker, and *Amnicola precursor* F. C. Baker. The depth of the water during that period was not over ten feet since *Valvata tricarinata* (Say), *Ferrissia fusca* (C. B. Adams), and *Helisoma anceps striatum* (F. C. Baker) were found in the living state by Baker ('35) in Itasca County, Minnesota, in water not over that depth.

Helisoma anceps striatum is more abundant in the north and its presence as a fossil in Illinois indicates colder water than now. *Gyrulus altissimus* (F. C. Baker) and *Menetus exacuus megas* Dall occurred at Chatsworth and also in the marl deposits of Itasca County. They were not found in the living state at the latter station. From the 2.5, 3.5, 4.5, 5, and 6.5 meter depths, fish scales were found which were identified as belonging to the family Centrarchidae which includes the basses, crappies and sunfishes.

DISCUSSION

Knowledge, in many instances, is lacking relative to how far the ice retrogressed before it advanced again during the various intraglacial periods. That data, if available, would be of great value in the interpretation of the pollen diagrams of bogs associated with the moraines. It may be possible that the ice during some of the intraglacial stages retreated far enough north to permit the development of forests on the newly exposed drift similar to those reported by Wilson ('32) for the period between Leverett's third and fourth substages of the Wisconsin. Forests may also have been in the proximity of the ice like those described by Cooper and Foot ('32)—“They flourished during late Pleistocene time, while the waning ice sheet still lingered within the present boundaries of the state.”

Concerning the Tazewell bogs the question may arise regarding their age in comparison with those of the Valparaiso drift of the Cary substage. The depressions in the Tazewell drift are doubtless as old as the drift itself. As stated before, the Bloomington drift is about ten thousand years older than the Valparaiso. It is possible that peat began to accumulate in these depressions at an early date, since conditions could have been similar to those described by Baker in connection with the life of Wilmette Bay. Much of the fauna which he found required peat-forming plants for their existence. Baker ('20) states: “The majority of the species are represented by a multitude of individuals showing that life was abundant during this period. All of the species are north temperate and boreal in distribution; many, indeed, extend as far north as the 60th and 70th degrees of North Latitude. It is not remarkable therefore, that this life should have followed so closely the retreating ice. The oak, spruce and other conifers are also indicative of a cold-temperate climate.” Cooper and Foot ('32) found the present flora within and around an Alaskan bog which is only a half mile from the Davidson Glacier in many respects like the plants whose fossil remains were found in a late Pleistocene peat deposit near Minneapolis. The peat of the Minneapolis deposit, as stated before, accumulated when the ice front was only a short distance away.

One would not be justified in saying that the climate was frigid in central and southern Illinois during the period when the ice was present within the confines of the state. The area now termed Illinois during late Pleistocene was not a center of ice accumulation like that of Labrador but rather a region

where forward movement took place as a result of ice deposition much farther north. During retreat, the ice itself did not move but the ice front melted back due to moderating temperatures. It was a region of comparatively thin ice, the ice dropping and passing over its own debris and thereby causing no removal of underlying drifts. This is evidenced by the fact that the best and most complete examples of superimposed undisturbed drift sheets of the entire Pleistocene period are found in the Mississippi Valley (Voss, '33) in contrast with the scanty drift records in Canada where the ice was much greater in thickness and the erosive effect more pronounced. Baker (unpublished paper) concludes from his studies of Pleistocene mollusca from loess deposits in north-central Illinois that soon after the retreat of the ice, the isotherm, which is now found at the Canadian boundary, was found in central Illinois.

Loess is often mentioned in connection with the history of postglacial vegetation, some writers being imbued with the misconception that dry conditions were necessary for its deposition. The problem regarding its origin and the conditions under which it was deposited, has been solved by much intensive work on the part of several geologists and biologists. Leighton ('33) has demonstrated that loess is thickest close to major river valleys; that its composition is practically identical with materials found in the valley-trains; and its deposition occurred while the streams were actively building up their banks with silty materials, semi-aridity being unnecessary.

Baker (unpublished paper) in his studies of a post-Normal deposit in the vicinity of Wyand, Bureau County, Illinois, states: "The presence of the small number of specimens of the little *Succinea* in the loess immediately overlying the gravel shows rather conclusively that the mollusks took possession of the territory very soon after the retreat of the ice and very early in the accumulation of the loess deposit." The species of *Succinea* which he found is now extinct and it suggested prairie or grassland conditions. These were followed by types which are characteristic of open boreal woodlands. As the loess increased in thickness, the number and variety of mollusks increased. Snails usually associated with well developed forests such as found at present in northern Minnesota and southern Canada appeared next. In the upper fossil-laden layers there occurred a few specimens of the mollusk which can now be found in the living state in Bureau County and its presence in the loess would suggest present day conditions. The top layers of the deposit unfortunately are nonfossiliferous due to leaching. Considering the above mentioned data, it is difficult to conceive that the loess, at least in Illinois, accumulated during a xerothermic period.

Regarding a xerothermic period, Fernald ('35) makes this statement: "Personally 'I am from Missouri' regarding this proposition. If *Ceanothus sanguineus*, *Woodсия oregona*, *Carex rossii* and other western xerophytes are interpreted as relics of colonies which extended across the Great Plains of Keweenaw in the reputed early arid spell, why have they so completely dis-

appeared from the great arid stretch of Plains, with their bluffs and crests, which should now suit them? They are accompanied in Keweenaw by western mesophytes, such as *Melica smithii*, *Corallorrhiza striata*, *Vaccinium membranaceum*, *Rubus parviflorus*, *Adencaulon bicolor*, and others. Would those who believe in the 'xerothermic' post-Wisconsin climate maintain that these mesophytes also crossed the Plains and reached Keweenaw during their 'xerothermic' stage? I cannot believe it."

The pollen diagrams of the Valparaiso bogs (Voss, '34) practically reveal a complete picture of the forests of post-Valparaiso times in Illinois. Unfortunately, the forest history of the post-Bloomington period is less complete due to the absence of satisfactory pollen records in the upper layers of the Tazewell bogs. As mentioned before, some of the Tazewell bogs may have reached the end of their peat-forming process long before the invasion of the Valparaiso ice. On the other hand, peat may have accumulated in the Tazewell depressions during both the Tazewell and Cary substages.

The succession of forests as shown by the pollen diagrams of bogs from both substages apparently is the same in most cases: (1) Increase and dominance of the conifers; (2) decline of the conifers and the advance of the deciduous forest. If the oldest layers of the Tazewell peat formed very slowly, the period of conifer dominance of that stage may coincide with the period of conifer dominance following the retreat of the Valparaiso ice. On the other hand, the post-Bloomington conifer forests might have been superseded by the deciduous before the advance of the Valparaiso ice-sheet and the succession of forests in central Illinois since Bloomington times could have been as follows: (1) northern conifer, (2) deciduous, (3) northern conifer, (4) deciduous.

If more data are obtained regarding the distance the ice retreated during each intraglacial period; if further pollen statistical work is done in localities having similar geological histories; and if additional studies are made of post-glacial loess deposits, the problems, such as the ones just mentioned, will be more easily solved.

SUMMARY

Pollen analyses of peat from nine bogs found in Tazewell drift were compared with those of younger bogs located in Cary drift. Some of the Tazewell drift is at least ten thousand years older than that of the Cary.

The early succession of forests following the retreat of the ice of the Tazewell and Cary substages was the same: (1) increase and dominance of the conifer; (2) decline of the conifer and the advance of the deciduous forest. Following the advance of the deciduous forest during post-Bloomington times, it may have been superseded by conifer and the conifer in turn replaced by the deciduous.

Aquatic snails apparently were responsible for the low pollen frequency of the marly peat.

No sphagnum was found in the Tazewell peat.

Stratigraphic studies of the mollusca from associated loess deposits are extremely valuable in the interpretation of climatic conditions.

Evidence supporting the theory of a xerothermic period during post-glacial times is lacking.

ACKNOWLEDGMENTS

Grateful acknowledgment is here made of my indebtedness, to Dr. George D. Fuller of the University of Chicago, for valuable suggestions and advice; to Dr. M. M. Leighton and Dr. George E. Ekblaw of the Illinois State Geological Survey, for geological data; to Prof. Frank C. Baker of the University of Illinois Museum, for the identification of Mollusca; and to Dr. D. F. Hansen of the Illinois State Laboratory of Natural History, for the identification of fish remains.

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POLLEN ANALYSIS OF TWO WISCONSIN BOGS OF DIFFERENT AGE

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In the summer and winter of 1934 the writer obtained peat samples from two peat bogs in the south central part of Wisconsin near the Wisconsin River (fig. 1). The first bog, which is hereafter referred to as the Dells bog, is located in the southeastern part of Juneau County, about two and one-half miles northwest of the city of Wisconsin Dells. The specific location is Section 14, T. 13 N., R. 5 E. This bog has been developed on the stream bed in an abandoned gorge of the Wisconsin River which occupied

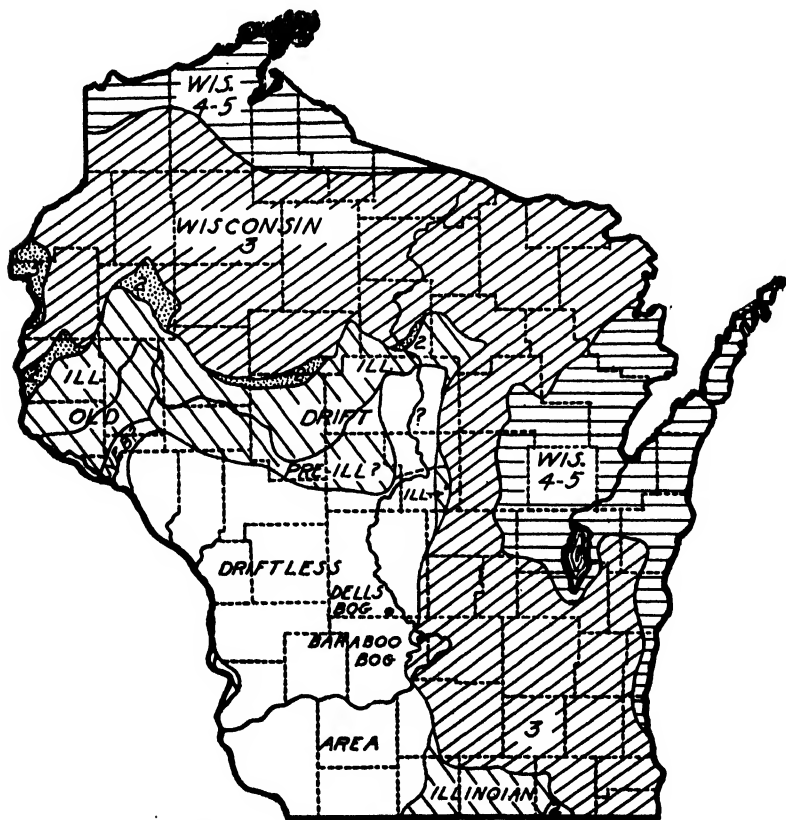


FIG. 1. Map of drift sheets of Wisconsin showing position of bogs. Compiled by F. T. Thwaites from maps of Leverett, Alden, and Thwaites, 1935.

this course in relatively recent postglacial time, according to Wisconsin geologists.¹ This opinion is apparently substantiated by the pollen spectrum as will be shown later. The second bog, which is referred to as the Baraboo bog, is located in the northeastern part of Sauk County about seven miles northeast of the city of Baraboo. This bog has been formed on the floodplain of Leech Creek which empties into the Baraboo River, which in turn debouches into the Wisconsin River near the city of Portage. The Baraboo bog is situated about four miles within the eastern edge of the drift deposited by the Third or Cary Substage of the Wisconsin glaciation. Although the bog covers an area of several square miles, the samples were obtained in Section 30, T. 12 N., R. 7 E. The two bogs are about fifteen miles apart.

The samples were taken at six inch intervals with a Davis peat sampler, labeled and wrapped in paper, and preserved in fifteen per cent alcohol. In the preparation of the peat for pollen identification, essentially the same method was used as described by Sears ('30). Two hundred or more pollens were counted from each level of the Wisconsin Dells bog, and one hundred and fifty or more in the Baraboo bog. The pollen frequency ran higher in the Dells bog than in the latter. In computing the percentages for tables and graphs, the half foot and the foot levels were added and the average used. The percentages are based on the total number of pollens counted including those that were unknown.

HISTORY AND CHARACTERISTICS OF THE BARABOO BOG

The Baraboo bog had its origin in a lake which inundated the floodplain of Leech Creek. During the melting and recession of the Third Substage of the Wisconsin glaciation, much water was released which caused the Wisconsin River to rise much higher than it is today. A large lake was impounded in the tributary valley occupied by Leech Creek as a result of the deposition of a vast amount of glacial outwash at its mouth which obstructed the normal drainage. The lake which was thus formed must have existed for a considerable length of time, because the lower two feet beneath the peat consist of sandy marl overlain with a foot and a half of marl sediment. In this marl is an abundance of molluscs, diatoms, bluegreen algae, and pollens of boreal plants which were probably blown in from the higher Baraboo Range to the south. Below these sediments are found sand and other coarser detritus deposited by earlier and swifter flowing streams. Including the marl deposit, the depth of the peat in the area from which the samples were obtained is about fifteen and one-half feet.

The elevation of the bog is from 800 to 820 feet and it is more or less continuous with large boggy areas which cover a large part of the Wisconsin River valley in this region. Dense stands of *Larix* cover a portion of the bog, while much of the rest is covered with sedge. The sedge areas are being invaded by *Cornus stolonifera*, *Rhus vernix*, *Betula pumila glandulifera*, and

¹ F. T. Thwaites, personal correspondence.

various species of composites including *Solidago* spp., *Aster* spp., and *Eupatorium* spp. Isolated patches of sphagnum can be found in the tamarack stands, but the bog has apparently long existed in the sedge-meadow stage. In the summer of 1934 the bog was very dry, and large tracts of the sedge areas had been mown for hay.

HISTORY AND CHARACTERISTICS OF THE WISCONSIN DELLS BOG

In a previous paper the writer discussed the time and method of origin of the bogs that exist in the driftless area of Wisconsin (Hansen, '33). About 1800 square miles of the driftless area in the south and central part of the state were inundated by Glacial Lake Wisconsin, formed during the recession of the Third Substage of the Wisconsin glaciation by the damming of the Wisconsin River at the Devils Lake watergap (Thwaites, '34). Thus there is a large area within the driftless area that is covered with outwash that was deposited by the glacial streams which flowed into the lake. The Dells bog exists within the bed of this glacial lake and must necessarily be postglacial. The abandoned river gorge in which the bog is formed was eroded during the drainage of Lake Wisconsin toward the end of the Wisconsin glaciation, and probably was not completed until quite late in postglacial time. When the river abandoned this channel, it left a small body of water in the gorge, in which the present day bog had its origin and subsequent development. The peat was deposited at a rapid rate as is indicated by the fourteen feet which have accumulated up to the present day.

At the time of observation the bog was covered with small areas of sphagnum, sedges, cattail, *Calla palustris*, *Larix laricina*, and shrubs consisting of *Betula pumila glandulifera*, *Alnus incana*, *Vaccinium canadense*, *V. pennsylvanicum*, *Gaylussacia baccata*, and *Pyrus melanocarpa*. On the cliffs, slopes, and other adjacent areas are *Quercus borealis maxima*, blueberry, *Ledum groenlandicum*, *Acer saccharum*, *A. saccharinum*, and *A. spicatum*, *Pinus strobus*, *Betula papyrifera*, *Tsuga canadensis*, *Pinus banksiana*, *Tilia americana*, *Amelanchier* spp., and other trees and herbs characteristic of the deciduous forest of this latitude.

SIGNIFICANCE AND CORRELATION OF THE POLLEN SPECTRA OF THE TWO BOGS

The geological history and physiographical setting of the Dells bog indicates that it is of relatively recent origin, whereas that of the Baraboo bog shows that it is of much earlier origin. These facts are further verified by the evidence furnished by the pollen spectra. If a bog located in this area had had its origin soon after the recession of the ice of the Third Wisconsin Substage, it would be logical to assume that in the light of past work in fossil pollen analysis (Voss, '34), that the lower levels would show a high percentage of boreal trees such as *Abies* and *Picea*.

Abies and Picea

The relative ages of the two bogs are perhaps best shown by the frequency of spruce and fir pollens in the lower levels (fig. 2, *D*). The lower two feet

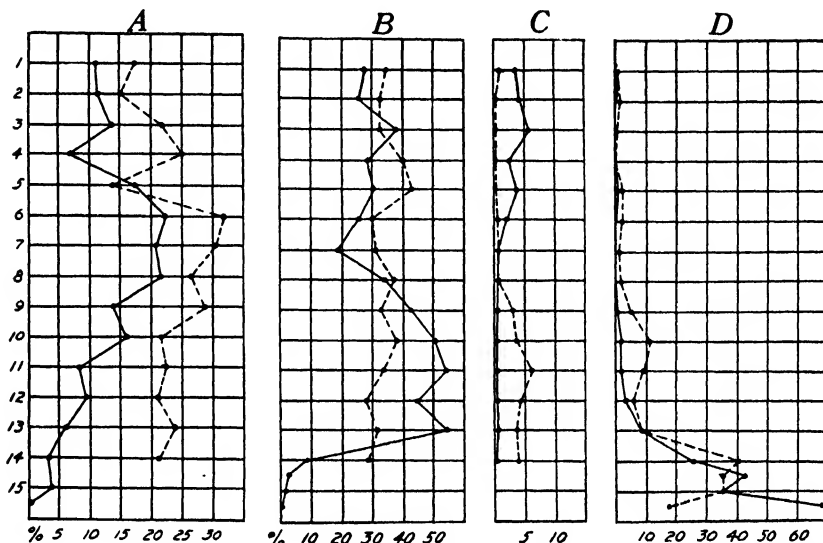


FIG. 2. Pollen diagrams. *A*, *Quercus* pollen, entire line Baraboo bog, broken line Dells bog; *B*, *Pinus* pollen, entire line Baraboo bog, broken line Dells bog; *C*, Dells bog, entire line Ericaceous pollen, broken line Cyperaceae pollen; *D*, Coniferous pollen, Baraboo bog, entire line *Abies*, broken line *Picea*. Depth of bogs in feet at left.

of the Baraboo bog have a high frequency of these two species. The lowest level at 15.5 feet shows 68 per cent *Abies* and 18 per cent *Picea* out of a total of 134 pollens observed. Spruce increases in the next three higher levels at the expense of the fir which practically disappears at 8 feet. This fact is probably to be correlated with the further retreat of the ice. Spruce also shows a decrease to 6 per cent at 12 feet indicating a continued tendency toward warmer and dryer climatic conditions, but increases to a frequency of over 9 and 10 per cent at the 11- and 10-foot levels respectively. This latter increase might be correlated with the advance of the Fourth-Fifth or Mankato Substage of the Wisconsin glaciation, causing a recurrence of a damper and cooler climate in this area. That this is probable is shown by the Two Creeks Forest Bed in Manitowoc County in the eastern part of the state (Wilson, '32). The study of this forest bed has shown that a spruce forest existed in this area during the period of deglaciation between the retreat of the Third Wisconsin Substage and the advance of the Fourth-Fifth Substage. During the readvance of the ice, the boreal forests which had followed the receding ice were forced again to retreat toward the east and south. Although the ice did not reach the Baraboo region, it came close enough to record its influence

by means of pollens in the bog. There is a gradual decline in the spruce pollen frequency from 10 feet to the surface. The higher parts of the Baraboo Range for a distance of about four miles east of Devils Lake were not covered with ice and may have supported a forest of fir and spruce, even while the adjacent areas were covered with ice.

A somewhat different story is indicated by the spectrum of the Dells bog, in which there are apparently no fir pollens and very few spruce pollens. This would tend to show that the Dells bog did not begin to form until most of the boreal forests had migrated east and out of range of pollen dispersal to the bog.

Pinus

Pine pollens from both bogs (fig. 2, *B*) consisted chiefly of *Pinus strobus* with some *P. resinosa* and *P. banksiana*. Very few *Pinus* pollens occur in the lower four levels of the Baraboo bog, but there is a sharp increase to 54 per cent at 13 feet probably because of a decrease in precipitation and an increase in the temperature as the influence of the receding ice of the Third Wisconsin Substage became less pronounced. Apparently pine was not influenced greatly by the advance of the ice of the Fourth-Fifth Substage of the Wisconsin glaciation. The frequency of pine pollen reaches its lowest point of 19 per cent at 7 feet, from which it increases with some fluctuations to 38 per cent at 3 feet, and then decreases to 28 per cent near the surface. The low frequency at 7 feet is probably to be correlated with a period of desiccation, because there is a striking increase in the frequency of grasses and composites at the same level.

In the Dells bog the *Pinus* spectrum does not show as much variation in frequency (fig. 2, *B*). The lowest level at 14 feet has a frequency of 29 per cent, which indicates that *Pinus* had already become fairly abundant in this area at the time of the origin of the bog. The same decrease noted at 7 feet in the other bog is also present here in the 6 and 7 foot horizons, which would tend to indicate that the peat deposited at this depth is more or less concurrent in time of deposition. There seems to be a fair amount of correlation throughout the pollen spectra of the two bogs.

Quercus

The spectra of *Quercus* pollens seem to correlate fairly well (fig. 2, *A*). Only a trace is found in the lowest level of the Baraboo bog, but there is a gradual increase up to 22.5 per cent at 6 feet, and then a sharp decrease to 7 per cent at 4 feet. At the time of initiation of the Dells bog, oak had become sufficiently abundant in this area to record a frequency of 21 per cent from which it gradually increases to its highest frequency of 32 per cent at 6 feet. This is followed by a decrease to 14 per cent at 5 feet, from which point it increases again to 25 per cent at 4 feet. Although these frequencies occur at 4 and 5 feet respectively in the two bogs, they may be correlated with

the same unfavorable conditions about the same time. It might be attributed to fire, insects or disease rather than a climatic factor.

Acer

This genus is represented by pollens from three species; *Acer spicatum*, *A. saccharinum*, and *A. saccharum*. The curves correlate closely throughout the entire spectra, with a gradual increase from the bottom to the top (fig. 3, C). The decreases to a frequency of .02 per cent at 11 feet in the Baraboo

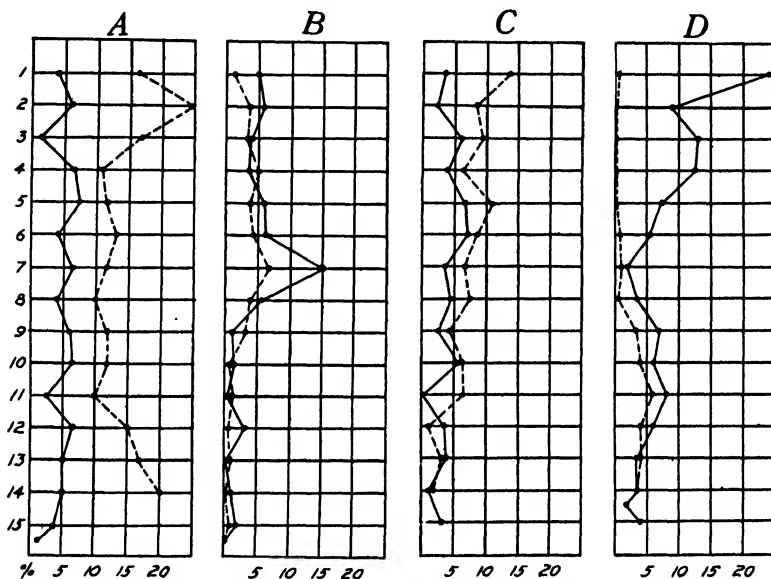


FIG. 3. Pollen diagrams. A, Betulaceae, entire line Baraboo bog, broken line Dells bog; B, Baraboo bog, entire line grass pollen, broken line composite pollen; C, *Acer* pollen, entire line Baraboo bog, broken line Dells bog; D, Cyperaceae, entire line Baraboo bog, broken line Dells bog. Depth of bogs in feet at left.

bog, and to 1.5 per cent at 12 feet in the Dells bog perhaps are to be correlated with the advance of the ice of the Fourth-Fifth Substage of the Wisconsin glaciation.

Betulaceae

The birch family is represented by four genera; *Alnus*, *Betula*, *Corylus*, and *Ostrya*. The spectra are surprisingly well correlated (fig. 3, A) in view of the fact that the pollen contributors are represented by some species which grow on the bog, and others which grow on higher ground adjacent to the bogs. *Alnus* is by far the most abundant, with *Betula* second. The birch probably consists chiefly of *Betula pumila glandulifera* which is common on both bogs at the present time, and is one of the most common shrubs on the

bogs located in the driftless and adjacent areas. There is a greater percentage of Betulaceae pollens in the Dells bog, and the type of peat would tend to indicate that the bog has existed in the shrub stage since early in the life of the bog. The Baraboo bog has existed in the sedge-meadow stage during a large part of its existence, and many of the pollens here represented are probably from white birch which grew in adjacent areas. In general, the pollen spectrum of this group would indicate changes in the bog complex rather than variations in the ecological conditions in the surrounding area.

Ericaceae

Ericaceous pollens are apparently present only in the Dells bog, where they become more abundant in the upper levels (fig. 2, C). The pollens of this group have had two sources; first, from *Ledum groenlandicum*, *Gaylussacia baccata*, and *Vaccinium pennsylvanicum* which grow on the sandstone cliffs adjacent to the bog, and second, from *Vaccinium* on the bog. The presence of these pollens, the type of peat, and the low frequency of sedge pollens show that the bog has had largely a sphagnaceous-ericaceous type of development.

Cyperaceae

Sedge pollens are far more abundant in the Baraboo than in the Dells bog; especially from the 7 foot level to the surface (fig. 3, D). The spectra indicate that both bogs had a fair amount of sedge present in their earlier stages. It soon began to die out, however, until at the 7 foot level the frequency decreases to 2 per cent in Baraboo bog and 0.2 per cent in the Dells bog. The deposition of peat at this level and in its vicinity, must have taken place during an exceedingly dry period (Sears, '30), as was previously shown to be indicated by the *Pinus* spectrum. The xeric conditions during this time must have been well enough pronounced to have lowered the water table in the bogs sufficiently to destroy much of the sedge. When a more humid climate followed, the Baraboo bog developed into a sedge-meadow type, whereas the Dells bog never recovered its sedge flora to any great extent. Instead, the increase in Ericaceae and Betulaceae pollens from the 7 foot horizon to the surface would tend to indicate that the bog was taken over by shrubs belonging to these two groups. The pollen spectra of Ericaceae and Cyperaceae of the Dells bog shows very clearly the transition from a sedge to a shrub stage, between the 7 and 6 foot levels (fig. 2, C).

Gramineae and Compositae

These two families are better represented in the Baraboo bog, perhaps because of the greater accessibility of pollens from plants in the surrounding area, as well as the larger size (fig. 3, B). Both groups in the Baraboo bog seem to correlate to some extent, but the abrupt increase to 15 per cent for

grasses and to 6.5 per cent for composites at the 7 foot level is especially to be noted. The decrease in *Pinus* and *Cyperaceae* at this level in both bogs strongly suggests the above mentioned xeric period or the destruction of the forests by fire. In the case of fire, the grasses and composites would have had an excellent chance to gain a foothold in the denuded area and get a good start before the forests would have been able to recover the area. Denudation by fire would tend to increase erosion and also the runoff of precipitation, thereby lowering the water table in the adjacent bogs. This would in turn have a decidedly unfavorable influence upon the sedge flora in the bogs. However, the fluctuations are probably a result of change in climate rather than that of fire.

Coniferous and Deciduous trees

Coniferous pollen in the Baraboo bog shows a greater fluctuation throughout the spectrum than those in the Dells bog (fig. 4, *A*). This is due to the

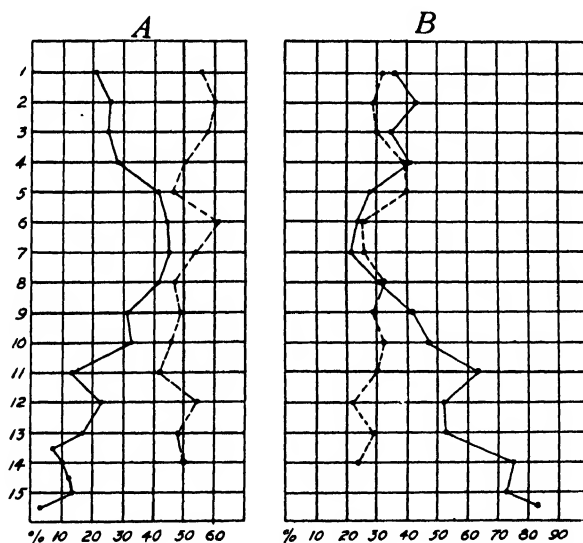


FIG. 4. Pollen diagrams. *A*, deciduous pollen; *B*, coniferous pollen, entire line Baraboo bog, broken line Dells bog. Depth of bogs in feet at left.

fact that the lower levels of the former bog contain a high percentage of fir and spruce pollens which came from the boreal forests which existed in this area before the Dells bog had its origin. The deciduous pollen likewise shows a similar condition in regard to fluctuation, with the variation reversed, with the deciduous pollens few in the lower levels of the Baraboo bog (fig. 4, *B*). The spectra for both coniferous and deciduous pollen in the Dells bog do not show nearly such wide variation, probably because the forests had reached a more or less static condition by the time of its initiation. The advance of the

ice of the Fourth-Fifth Substage of the Wisconsin glaciation seems to be reflected by an increase in the coniferous pollens and a decrease in the deciduous pollens at the 11 foot level in both bogs. The hypothetical xeric period is conversely reflected by both groups at the 6 and 7 foot horizons. The general trends in the upper levels would tend to indicate a moderation of the climate in recent and present times, with neither extremely xeric nor extremely humid conditions.

CORRELATION OF THE AGES OF THE TWO BOGS

As previously pointed out the geological and paleobotanical evidence points to the fact that the Baraboo bog is considerably older than the Dells bog. There is also evidence offered in the pollen spectra of the chief pollen groups which indicates that some correlation can be made as far as the time element is concerned.

The depths of the peat in the area of sampling is 14 feet in the Dells bog, and 15.5 feet for the Baraboo bog. The lower two feet of the Baraboo bog consists of about six inches of sandy marl, and one and one-half feet of marl, so that the deposits of peat formed of actual plant material are approximately the same in both bogs. The peat at the same foot levels, however, is not necessarily exactly the same in time deposition. It would seem that the two feet of marl represents the amount of deposition that occurred during the time which elapsed between the recession of the Third Substage of the Wisconsin glaciation and the initiation of the Dells bog. This length of time must represent a fairly large portion of the present postglacial period, because the deposition of marl takes place at a slow rate. Although the ice of the Third Substage had receded far enough north and east to allow the migration of flora into the Baraboo region, the amount of glacial water was tremendous. Glacial Lake Wisconsin was still in existence during the Fourth-Fifth Substage, but at a lower level than before so that the Wisconsin River could have eroded the now-abandoned gorge in which the Dells bog is formed. After the waning of the later stages of the Wisconsin glaciation, Lake Wisconsin persisted until the Dells were eroded and the river occupied this channel as long as there was sufficient water available to require the use of both the present and previous channels. The upper limit of the marl deposit then, is undoubtedly to be correlated with the time that the ice of the Fourth-Fifth Substage had receded sufficiently to decrease the amount of water in the main streams and cause the partial drainage of standing water such as existed on the floodplain of the present day Leech Creek. Simultaneously with the drainage of these areas must have occurred the abandonment of the gorge of the Wisconsin River and the beginning of the subsequent development of the Dells bog. In the writer's estimation almost half of the Third Wisconsin postglacial time must have elapsed before the initiation of the Dells bog. In view of this reasoning, the bogs have had about the same rate of peat formation, excluding the two feet of marl in the Baraboo bog.

The pollen spectra of the chief groups would indicate that the various

TABLE I. Percentages of principal pollens from the Baraboo Bog *

Depth Ft.	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	<i>Tsuga</i>	<i>Larix</i>	<i>Quercus</i>	Betulaceae	<i>Acer</i>	<i>Tilia</i>	<i>Carya</i>	<i>Juglans</i>	<i>Ulmus</i>	<i>Salix</i>	Cyperaceae	Gramineae	Compositae	Other Monocots
1		0.3	27.8	1.1	10.2	11.0	3.5	3.0	1.1		0.4	0.4	0.2	24.0	5.0	1.0	0.8
2		1.7	26.0	0.3	7.3	11.5	6.0	2.2	0.5			0.5		9.0	5.5	4.0	0.3
3		0.4	38.5	0.7	5.7	14.0	1.5	6.0	1.2				0.3	13.0	4.0	3.5	3.1
4			29.0	0.3	11.8	7.0	6.5	4.0	1.6				1.3	12.5	3.7	5.0	0.3
5	0.5	1.8	30.2		1.3	17.5	7.5	6.5	2.7		0.8	0.5		7.5	5.7	4.2	1.0
6		2.1	26.0	0.5		22.5	4.5	7.0	1.9	0.2		2.0	0.5	5.5	6.0	4.5	0.5
7		1.0	19.0			20.5	6.5	3.5	7.3		0.2	0.9	0.2	2.0	15.0	6.5	0.6
8		2.0	33.0	0.5	0.2	21.5	4.5	4.5	3.6	0.6		0.2	0.4	3.0	5.5	4.0	0.2
9	0.7	5.3	42.6		0.4	14.0	6.0	2.5	2.9	0.4		0.8	2.5	7.0	1.5	3.0	2.5
10	1.9	10.3	50.4			16.0	6.5	5.5	3.3			0.5	0.2	6.0	2.0	1.0	
11	2.0	9.4	54.1	0.3	1.5	8.0	2.5	0.2	2.1					8.0	0.7	1.2	1.8
12	3.0	6.0	45.0	1.1	1.4	9.5	6.5	3.5	1.6			0.5		6.0	3.0	0.7	1.4
13	9.0	9.0	54.2		0.4	6.2	5.0	4.0	0.4					3.5	1.0	0.5	0.7
14	26.0	40.4	9.0			3.0	5.0	1.0						3.5			0.6
14½	42.0	36.8	3.0		1.4	3.0								1.0		2.5	0.7
15	36.0	36.4	1.2			4.0	4.0	3.0						2.0	2.0	0.5	0.7
15½	68.6	18.0			1.5	0.2	1.5							4.0			

* Percentages based on total number pollens counted, including unknown.

TABLE II. Percentages of principal pollens from the Wisconsin Dells Bog *

Depth Ft.	<i>Picea</i>	<i>Pinus</i>	<i>Tsuga</i>	<i>Larix</i>	<i>Quercus</i>	Betulaceae	<i>Acer</i>	<i>Tilia</i>	<i>Carya</i>	<i>Juglans</i>	<i>Ulmus</i>	<i>Salix</i>	Ericaceae	Gramineae	Compositae	Amaranthis Chenopods	Cyperaceae	Other Monocots
1		34.4	0.9		17.5	16.0	14.0	1.3	0.7	0.4	0.2	0.4	3.5	0.7	1.1	0.4	0.2	3.1
2		33.5	0.3	0.5	15.2	26.0	8.5		0.1	0.3	0.3	0.1	4.5	0.1	2.4			2.5
3		33.3	1.5		22.0	17.0	9.5			0.4	0.4	0.4	5.5		1.9	0.4		0.9
4		40.1	1.6		25.0	11.0	6.5		0.9	0.4		2.2	2.5	0.2	3.2			2.1
5		43.0	1.5		14.0	12.0	11.0	0.5	0.2	0.3		2.6	3.7		1.7	0.3	0.4	1.6
6		30.0		0.4	32.0	13.0	8.5		0.4	0.4		0.6	2.2		3.9	0.4	0.4	1.7
7		31.6	0.5	0.2	30.5	12.0	7.0	0.7	0.2	0.4		0.4	0.5		2.5	0.6	0.4	2.2
8		37.1		0.2	26.5	10.0	7.5	0.8	0.2	0.4		0.2	0.2	0.2	2.1	0.2	0.2	0.5
9	0.5	33.0	0.4		28.5	12.0	4.5	0.2	0.2	0.6	0.2	0.2	0.5		1.1	0.4	3.1	
10	1.0	38.6			22.0	12.0	6.0	0.3	0.2	0.6			0.2		3.0	0.7	3.6	
11	1.7	33.5	0.4		22.5	10.0	6.5	0.3		0.3			0.2		3.0	0.3	6.2	0.4
12	1.2	28.3	0.2		21.0	15.0	1.5	0.1	1.2	0.1		2.6	0.5		4.4	0.7	4.4	0.4
13	2.5	31.0	0.2		24.0	17.0	3.5	0.5	0.5			1.7	0.2	1.0	5.0	0.2	3.7	0.6
14	1.2	29.0	0.2		21.0	20.0	2.0	0.4	0.2			0.2	0.2	3.9	5.0		4.0	3.6

* Percentages based on total number of pollens counted, including unknown.

ecological changes which occurred from time to time, are reflected in the same manner in each bog. The greater variations in the curves of the graphs are pretty well borne out in both bogs. These fluctuations are reflected in or near the same levels, showing that the rate of peat formation was equal in both bogs, and that some levels at the same depth are approximately the same age.

POSTGLACIAL CLIMATIC FLUCTUATION

The interpretation of postglacial climate from the pollen spectra is to be based upon certain critical groups, which would include *Picea* and *Abies*, *Pinus*, deciduous trees, and composites and grasses. *Quercus* would be the more important among the deciduous trees. Fuller ('35) divides postglacial forest succession of the mid-lake region into three periods, viz. (1) a period of establishment and relatively rapid decline of the boreal types, indicating a period of increasing warmth; (2) a long period of dominance by deciduous forests, indicating a period of maximum warmth; and (3) a period of slight increase in the boreal types, and a corresponding decrease in the deciduous trees, possibly indicating a period of decreasing warmth. This same sequence seems to be borne out for the greater part in the record of the Dells and Baraboo bogs, with the exception of that of composites and grasses. If composites and grasses are to be considered as xerothermic indicators, it would seem that the period of maximum warmth became rather xeric at the time represented by the highest percentages of these groups. The presence of relict prairies in the original vegetation of the driftless area (Shantz, '36) would tend to bear out this assumption, although the data from only two bogs would hardly be sufficient to warrant any definite conclusions. There seems to be no definite increase in the boreal types in the last period, but a slight decrease is shown in the deciduous trees since they reached the maximum during the second period. The deciduous forests have apparently remained much the same during the last two periods of postglacial forest development.

SUMMARY

1. Peat samples were obtained from two bogs about fifteen miles apart in the south central part of Wisconsin. One of them is located on the Third Wisconsin Glacial Drift, and the other is in the Driftless Area, within the bed of Glacial Lake Wisconsin.

2. The Baraboo bog was formed in a floodplain lake which was formed during the recession of the Third or Cary Substage of the Wisconsin glaciation. This lake probably existed throughout the rest of the Wisconsin glaciation.

3. The Dells bog was formed in a recently abandoned postglacial channel of the Wisconsin River. The depth of the peat in the center of the bog is 14 feet.

4. Geological evidence shows that the Baraboo bog is much older than the Dells bog. This evidence is further corroborated by the fossil pollen analysis

of each bog, as shown by the close correlation of the pollen groups in the respective bogs. • The two feet of marl deposit in the Baraboo bog represents a large part of postglacial time, while the actual peat deposits in each bog are contemporaneous with each other.

5. The postglacial plant succession had reached the *Quercus-Pinus* stage when the Dells bog had its origin, whereas it was in the initial stage of *Picea-Abies* when the Baraboo bog began its development.

6. The Dells bog represents a sphagnaceous-ericaceous type of bog, whereas the Baraboo bog has been a sedge-meadow type throughout the greater part of its existence.

7. A return of spruce forest may be recorded at the 11 and 10 foot levels in the Baraboo bog, which is further reflected by a decrease in the deciduous pollen in both bogs at 11 feet. This may have occurred as a result of the advance of the Fourth-Fifth or Mankato Substage of the Wisconsin glaciation which caused a recurrence of a damper and cooler climate.

8. A xerothermic period may be recorded at the 7 foot horizon in both bogs by a sharp decrease in the frequency of pine and sedge, and an increase in the composites and grasses at the same level in the Baraboo bog.

9. The results here obtained seem to agree to a large extent with other fossil pollen analysis which has been made in Wisconsin, Illinois, and Michigan.

10. This work tends to show that the evidence offered by fossil pollen analysis may be correlated to some extent with geological history.

The author wishes to express his appreciation to Dr. N. C. Fassett of the Botany Department, University of Wisconsin, for suggestions and criticisms, and to Mr. F. T. Thwaites of the Geology Department for suggestions and verification as to geologic statements.

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REVIEWS

RANGE PROBLEMS AND THEIR SOLUTION

In 1878, with bison on the way out and cattle of the white man on the way in, Major John Powell¹ presented a sensible plan for the development and use of western lands. Twenty years later, with the situation still far from hopeless, Pound and Clements² called attention to the ecological basis of land utilization in the grass country. Shortly thereafter Johnson³ emphasized the precarious character of the biological equilibrium in this region and the need for intelligent measures in its development. There is no reason to believe that any attention whatever was paid to the recommendations of these competent technical men. And in 1901 C. L. Shear⁴ submitted to the Secretary of Agriculture recommendations for a policy of government control of grazing land to be incorporated in Bulletin 25 U. S. D. A. This report contained explicit statements of the character and source of damage resulting from exploitation. It was never published, but instead, was returned, endorsed "All too true, but not best for us to take position just now. J. W."

The two monographs before us for review are workmanlike tributes to the vision of these several prophets of disaster.⁵ They are, for all of their scrupulous scientific cast, documents in the world's library of tragedy.

Thornthwaite has employed the technique of geography and climatology in an actuarial consideration of the hazards of the semi-arid short grass country. This is the region grading eastward from the Rocky Mountains into the humid prairies. "It is an area where climatic conditions unfavorable to a permanent agricultural economy occur with irregular persistency." The highly speculative character of farm operations in convincingly demonstrated in terms of climate, economics, and sociology. The most hopeful solution

¹ Powell, John W. 1879. Report on the lands of the arid region of the United States, etc. *U. S. Congr. 45, 2nd Sess., Exec. Doc. 73*, pp. 195.

² Pound, R. and F. E. Clements. 1900. *Phytogeography of Nebraska. Lincoln, Neb.*

³ Johnson, Willard D. The high plains and their utilization. *U. S. Geol. Surv., 22nd Ann. Rept. 1900-1901. Part IV. Hydrography*, pp. 637-669.

⁴ Shear, C. L. 1936. The conservation of public lands. *Science* 83: 204-205.

⁵ Thornthwaite, C. Warren. 1936. The Great Plains. [Chap. V in *Study of Population Redistribution: Migration and economic opportunity.*] *Univ. of Penna. Press*, pp. 202-250, illus.

Clapp, Earle H., et al. 1936. The Western Range. A great but neglected natural resource. [Report from Forest Service, transmitted as a letter from the Secretary of Agriculture.] *Senate Doc. 199. 74th Congress, 2nd session, 1936*, pp. xvi + 620, illus.

is believed to lie in reversion to a pastoral economy on a basis too large for the individual farm owner, and until that is accomplished the two alternatives that remain are either "permanent poverty and distress or permanent subsidy."

Senate Document 199 is the handiwork of a large committee of the Forest Service, organizing into sequent chapters an immense fund of information which that Service has acquired in the course of its prolonged study of the grazing problem. The area involved is 728 million acres, or nearly 40 per cent of the total land area of the United States, and comprises about three fourths of the land whose irregular eastern boundary lies close to the 99th meridian. "The major finding of this report . . . is range depletion so nearly universal under all conditions of climate, topography, and ownership that the exceptions serve only to prove the rule." The difficulties of an adequate solution are fully dealt with, and the specific recommendation made that supervision of the public domain—so far as it represents a biological resource—be transferred to the Department of Agriculture. In this many ecologists will be inclined to concur.

The book itself is remarkably organized and well written. The chapter on the Virgin Range (by R. E. McArdle and D. F. Costello, 71–80), for example—and with no disparagement to the rest—is a superb example of scientific exposition and description. The whole work is an invaluable manual, not only for the scientist, but for the publicist and man of affairs who may be concerned with the future of the Great West.

If these two monographs are not to become mere Humpty-Dumpty literature it behooves every ecologist in the country to exert himself. In spite of the general interest in intelligent conservation there is a tremendous inertia and reaction to overcome.

P. B. SEARS

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BIRDS AND OCEANOGRAPHY¹

If ecology is defined as the relation of life to environment, then Murphy's two volumes on sea birds must be dubbed the peer of all ecological studies using birds as basic material. Perhaps this is due to the relative uniformity of an oceanic environment. Without minimizing in the least the great complexity of physical factors with which the author has dealt in establishing correlations between winds, hurricanes, ocean currents, temperature, pressure, radiation, food-chains and the like, and the distribution and speciation of the 183 forms of birds monographed, it must be admitted that physical characteristics are more uniform over large areas and gradients are less abrupt in

¹ **Murphy, Robert Cushman.** 1936. *The Oceanic Birds of South America. American Museum of Natural History.* 2 vols. xxiv + 1245 pp., 80 figs., 16 col. pl., 72 half-tone pl. \$10.50.

an oceanic situation than in most terrestrial environments. Dr. Murphy is to be congratulated on making the fullest possible ecological use of an avian subject ideal for the purpose.

More than one quarter of the work is devoted to the physical environment. In some 70 pages the meteorology and hydrology of that quarter of the southern hemisphere in which South America lies are discussed in detail and illustrated with numerous maps, charts and diagrams. In 200 pages devoted to a hypothetical "circumnavigation of South America," the pelagic and offshore islands as well as the littoral are described in passages as excellent from a literary point of view as they are accurate scientifically. In the remaining 900 pages all of the penguins, albatrosses, petrels, tropic-birds, pelicans, boobies, cormorants, frigate-birds, gulls, terns, and certain of the ducks and shore-birds that occur in this section of the world are exhaustively monographed with respect to their nomenclature, taxonomy, distribution, phylogeny, their habits of feeding, nesting and migration, and their relations to each other and their environment. It is interesting that Murphy says in his introduction, "to those biologists that affect to believe that taxonomy is a finished or fruitless field for research, I must state . . . that it is still the uncompleted foundation for what ever we may hope to learn in ornithology."

One can only mention briefly some of the ecological highlights. The muddy waters of the Orinoco and Amazon drainages act as barriers to the southern extension of West Indian Brown Pelicans which being primarily littoral are unable to fly out far enough to sea to round the region of opacity and reach the clear waters of Bahia that would be eminently suitable for them. The periodic late summer hurricanes of the West Indies sometimes carry sea birds as waifs many thousands of miles and are responsible for the extension of range of West African boobies, tropic-birds and frigate-birds to American shores while preventing the extension of typically American birds to the east.

Sixteen stunning colored plates by F. L. Jaques are illustrative of habitats and associations rather than being merely portraits of birds. The additional 72 half-tone photographs of birds and land- and sea-scapes stamp this as one of the best illustrated bird books of all time. The work is fittingly dedicated to Dr. Frank M. Chapman, dean of American ornithologists.

The fundamental plan of the work is somewhat unusual in that certain arbitrary taxonomic units from a definite geographic area are accorded a primarily ecological treatment. The result will probably be more satisfying to the ecologist than to the systematist or the student of geographical distribution. No taxonomic unit is treated in its entirety. For instance, ten of the seventeen known forms of penguins are monographed, as are one species each of *Chlœphaga* and *Anas*, both of which genera of ducks have related species in South America less addicted to salt water. The reviewer regrets that such a compromise of taxonomic, geographical and ecological methods of attack should have been necessary. The title, "The Oceanic Birds of South America," is somewhat of an anomaly since, of those birds that are

resident in the area, by far the majority are confined to islands, either coastal or those of the high seas, while the periodic visitors are almost entirely pelagic. However in spite of these criticisms of the selection of material, it is hoped that from Murphy's talented pen may come further monographs of the oceanic birds of other continents.

RUDYERD BOULTON

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FORESTS IN FLOOD CONTROL ¹

The specific purpose of this 70-page bulletin is to summarize recent experimental evidence as a basis for counteracting implications or expressions by various groups of engineers, geologists and meteorologists regarding beneficial forest influences. The chief factors influencing normal run-off are listed as character of precipitation, geology and topography of the surface, and the vegetation cover. Since the last is the only one subject to human control it is necessary to understand as fully as possible how it operates. Specific data are given on interception of precipitation, retardation of melting snow, reduction of soil evaporation, absorption of water, influence of forest litter and of organic matter, effect of soil life, water percolation, and absorption of water. The conclusion is made that the climax forest of a region, valuable as it is in controlling run-off and erosion, may be subject to improvement by such measures as terracing, ditching, water spreading, check dams, stream rectification, etc. The consequences of disturbing forest cover, the relationship of ownership to watershed conditions, and a program for adequate watershed protection are well presented. A few typographical errors are scattered through the bulletin and "vegetative" is used in place of "vegetation" but these are minor errors in a bulletin which is particularly valuable because the discussion and conclusions are well supported by numerous facts acquired through research.

HERBERT C. HANSON

NORTH DAKOTA AGRICULTURAL COLLEGE, FARGO

A KEY TO THE GRASSES OF MONTANA ¹

The increased interest in pastures and grassland has led to a greater need for better facilities for identifying grasses by the average investigator. Most of the observations and investigations of grasses are made in their immature stages of growth so that keys using definite recognizable vegetative characters from which the different species can be readily identified are espe-

¹ Munns, E. N. and Ivan H. Sims. 1936. Forests in flood control. *Supp. Report Comm. on Flood Control, House of Repr., 74th Congress. U. S. Gov't Printing Office. Washington.*

¹ Hitchcock, C. Leo. 1936. A Key to the Grasses of Montana. 28 pp., 8 pl. *Publ. by the author, 50 cents.*

cially valuable. One of the latest booklets of this character is a "Key to the Grasses of Montana" by C. Leo Hitchcock, Associate Professor of Botany, University of Montana.

The booklet contains descriptions of about 200 species and has exceptionally good drawings for 185 species, containing perhaps the largest number of species described by vegetative characters. The key is easy to use, is very brief including only the conspicuous characters. This combined with the drawings should make the identification of grasses by their vegetative characters rather simple by using an ordinary lens.

A. E. ALDOUS

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SPECIATION¹

The time seems ripe for the first comprehensive analysis of modern knowledge of evolutionary events which brings the recent discoveries of the taxonomists, animal geographers, ecologists and geneticists into a balanced relationship. This book is a critical evaluation of an enormous scattered literature in a field that badly needs coordination. Every student of evolution will certainly find a wealth of source material in the bibliography and a well digested and critical discussion of the salient factors contributing to the evolutionary process.

The ecologist will be particularly interested in the discussions of distribution, isolation and natural selection. In such fields as protective coloration and mimicry, the reviewer finds the discussion avoiding both the propagandistic tendency of the biased advocates of the theories and the ignorance of the facts so often manifested by the critics of these concepts.

The chapter on correlation is pertinent, particularly as students of speciation so often fail to utilize statistical methods in the treatment of data, the significance of which is only to be judged through the use of mathematical tools.

Although genetical and cytological factors are included, I am inclined to feel that the mass of evidence accumulated by the geneticists in particular deserves a proportionally larger space than it receives. In as much as most books on evolution tend to place more emphasis upon the genetical factors than upon the ecological factors, however, it is filling a greater need to reverse the emphasis.

One is bound to find weaknesses in any such comprehensive treatment of a complex problem and doubtless many books will have to be written before the existing knowledge is brought together in a perfectly balanced perspective. The reviewer is aware that it is far easier to pick faults in such a work than it is to produce a volume which is free from error.

¹ Robson, G. C. and O. W. Richards. 1936. *The Variation of Animals in Nature*. Longmans, Green and Co. 425 pp., 30 figs., 2 col. pls. \$8.25.

An evolutionary tendency of almost universal importance is that of degenerative change and possibly the cave faunas illustrate convergence of degenerative modifications better than the animals inhabiting any other ecological habitat. The problems are briefly referred to in the book, but the analysis of the data hardly seems as critical or as thorough as the treatment of less important problems.

The last chapter entitled "Conclusions" emphasizes a mystical teleology that seems somewhat out of harmony with the severely critical treatment in the body of the book. Possibly the reviewer has misunderstood the philosophical implications of such sentences as the following: "If this organising activity is indeed an agent in producing the main adaptive tendencies in evolution, it might be argued that the gradual upbuilding and perfection of adaptations, because they involve so large an element of design, must also involve some reference to a purpose independent of survival value and chance, and existing as an end in itself."

I must also mention my surprise at the price of the book. Neither its length nor illustrations would seem to justify a cost that is about twice that of comparable works.

Even with these criticisms, the reviewer is genuinely enthusiastic about this book and feels that it is indispensable to every scholar who finds himself confronted with aspects of evolution.

ALFRED EMERSON

THE UNIVERSITY OF CHICAGO

THE PREPARATION OF SCIENTIFIC PAPERS¹

Editors of scientific journals are constantly surprised at the errors which are to be found in the majority of the manuscripts submitted for publication. Often the tables and citations are not checked against the original data, captions for the figures and summary paragraphs are not included, and scientific names are incomplete or inaccurate. Probably the worst fault is the tendency to repeat statements and to include unnecessary sentences. Both experienced and inexperienced authors are likely to submit manuscripts which could be radically reduced with improvement. The desire to have many published papers results in preliminary reports which would often be best delayed until the complete data are collected. Unfortunately, many journals cannot afford to publish long articles with many illustrations. This fact forces the authors to break up their papers into smaller sections and submit the manuscripts to different journals. Such a practice adds to the inefficiency of bibliographical reference. It is not unusual to find that authors have re-worked practically the same data into several papers for publication in several journals already struggling to use their budgets for the most efficient service to their subscribers.

¹ Trelease, S. F. and Emma S. Yule. 1936. Preparation of Scientific and Technical Papers. *The Williams & Wilkins Co., Baltimore*, 125 pp. \$1.50.

Such practices hamper the editorial boards, increase the cost of publication, and interfere with the efficient increase in scientific knowledge. Delay in publication is the immediate result.

The editors of *ECOLOGY* are convinced that authors would receive better service in the publication of serious research if they would refer to the small book by Trelease and Yule while preparing their papers. Reference to the journal would acquaint them with the special styles and forms which characterize each periodical.

ALFRED EMERSON

THE UNIVERSITY OF CHICAGO

THE SOIL IN THE FIELD¹

The increasing necessity that the field ecologist, whether concerned principally with the plant or with the animal life, should become familiar with the soil makes the present small volume a welcome addition to his equipment. It comes from the University of Oxford, England, and presents in a nontechnical manner directions for the intelligent study of soil in the field according to methods used by modern soil scientists. By its use the results of such investigations may be presented in such form that they may be more useful and more widely intelligible. Considerable space is devoted to the necessary definition and explanation of the terms of modern pedology and to their application to soil surveys.

Some idea of the contents of the book may be had from the headings of its five chapters: Soil site characteristics; Soil profile description; Soil sample collection; Mapping of soils; and Notes on various soil survey systems.

The size of the volume will make it convenient to slip into the pocket and the organization of its contents will facilitate easy reference. More diagrams would have been an improvement and a short bibliography should have been added.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

¹ Clarke, G. R. 1936. The study of the soil in the field. 142 pp. *Oxford University Press, New York*. \$1.75.

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NOTES AND COMMENT

ECOLOGY AND THE INDIANS

If ecology may be defined as "the relation between organisms and their environment," that gives me leeway to discuss the entire Indian problem from Home Economics to Liquor Suppression and from Christopher Columbus to John Collier.

When Columbus discovered America, there were, as closely as we can calculate, about 750,000 people living in the 1,903,000,000 acres of what is now the United States. This was ample land to support these people in safe equilibrium with both the plants and animals of their environment. Of course then as now, there were sporadic droughts which worked temporary local hardships. There were game cycles and game migrations which brought starvation to many individuals. But there was no lasting impairment of the natural resource. There is, for instance, almost no indication of accelerated erosion prior to the advent of the white man, although it is probable that such erosion did take place around certain ceremonial grounds where the Indians concentrated in abnormal numbers. However, there was sufficient space available that if one area became over-used, there was plenty of room for a tribe to move to other uninjured sections. Tribal wanderings sometimes brought neighboring Indians into contact and warfare, but it did not result in any serious deterioration of the natural resource.

As soon as the first Spanish settlements occurred in what is now the United States, the area available for the Indians became somewhat restricted. Nevertheless, for many decades after the founding of St. Augustine and Santa Fe in the 16th century, the area occupied by the white people was not sufficient to interfere seriously with the established pursuits of the Indians. Even at the close of the Revolutionary War, aside from the tribes along the Atlantic seaboard, the great bulk of the Indians on the continent were not affected. When the Lewis and Clark expedition crossed the continent in 1804-1806, they found few signs of white influence among the tribes, and no signs of Indian land shortage.

But land shortage was not slow in making itself felt after the passage of this memorable expedition. All through the 19th century the white pioneers swarmed into one hunting ground after another on which the Indian economy depended. Eastern tribes were pushed westward, and crowded upon even the most remote Indians. Many tribes which had never seen white men felt the influence of the white invasion in this indirect manner.

This pushing westward of tribes profoundly affected their economics. The Sioux, whom we generally think of as one of the most war-like and migratory tribes, were not particularly war-like and were fairly stable before the advent of the white man. They depended a great deal on agriculture for their livelihood. When the white migration drove them from their fertile land east of the Mississippi, out on the plains where agriculture was much more difficult and where they had to displace other Indians who did not want to be displaced, they had to change their whole mode of living. They became a nation of hunters and warriors.

In 1886, Geronimo and his Apache followers were finally rounded up by the United States Army, and the last important unconquered Indian tribe was brought under subjugation. Virtually all of the Indians were safely cooped on definitely limited reservations. The total area embraced in these reservations amounted to 138,000,000 acres. This, although only a fourteenth part of what the Indians possessed three centuries before, might nevertheless have been enough to support their diminished population if it had been

conserved and administered to yield them the maximum possible permanent wealth. Unfortunately it wasn't. The very next year, in 1887, a disastrous law was passed by the combined efforts of sincere altruists and unscrupulous marauders. The altruists believed that Indians were as good as white men and therefore that each Indian should be made an individual owner of land as the white man owned his land. The marauders realized that the altruists' objective was beautifully designed for the cheap and legal grabbing of the land from the Indians. The result of this concerted action was the Allotment Act which gave the individual Indians of most tribes from 80 to 640 acres in personal ownership. Through this personal ownership the Indian estate was reduced from 138 million acres in 1887 to 48 million acres in 1933. The cause of this disastrous dissipation of their resource was that when the Indians got their land in private ownership, together with the right to sell it for immediate cash, most of them sold. This was natural because they had been raised in an economy where today means almost everything and there is little use of worrying about the incalculable tomorrow.

There was also another reason for this dissipation. Most of the reservation land was valuable only for its forage or its timber. In the arid West, with single water holes required to serve thousands of acres and with the necessity of providing for all livestock both low lying country for winter range and mountainous country for summer range, it is generally impossible to use land in units smaller than 5,000 acres. The average allotment did not average a twentieth part of that size. When the original allottee died and the interest in the allotment was further subdivided among numerous heirs, the only value the Indians generally could derive from such lands was to sell them. Similarly with the use of timber lands, a single allotment was not nearly large enough for an Indian to operate and amortize his investment in sawmill and logging equipment, even if he had the experience to do so and the cooperation of the Indian Service, both of which were generally lacking. It is true that there were some reservations, especially in the Southwest, where allotment never took place. Here the Indians were generally able to develop a higher standard of living and a less confused social life than where the areas were divided.

However, divided or undivided, the 328,000 Indians who are today living in the United States do not have enough land to support themselves. That is true even though a small fraction of these Indians make their living away from reservations. It would also be true even if the irrigation possibilities of these reservations were developed to the limit. The 48 million acres of Indian lands consist by and large of the poorest lands yet remaining in the United States. If they had been anything else, they would probably not have been set aside as Indian reservations, or if set aside, the white men would have gotten them through the workings of the allotment system.

The chief economic value of about 75 per cent of the present area of Indian reservations is for the raising of livestock. As a result of not having enough land to support themselves adequately, the Indians tend to concentrate more livestock on their ranges than can be supported on a permanent basis, and, similarly, they have in the past logged many of their timbered reservations more heavily than sustained yield management would permit. The effect of such overgrazing and such overcutting has in some cases been disastrous. The best known example is the Navajo Reservation, where there are at least twice as many sheep and goats as the range will support, and in spite of the desperate efforts of the government to induce these Indians to reduce the number of their livestock. This terrifically overgrazed Navajo reservation shows worse and worse forage each year, and every year millions of tons of soil are washed away into the Colorado River.

Unlike the Navajo Reservation, where the Indians utilize every acre of their territory themselves, on most reservations the Indians still lease a considerable fraction of their land to white men. This bad habit has been developed over a period of many years.

Economically it is bad for the Indians because when they lease they only receive the rental value of their land while white men get the benefit of the wages and the profit which comes from its use. Socially it is bad because men who make their living without working for it generally seem to degenerate physically and morally. It is one of the most important objectives in the program of John Collier, present Commissioner of Indian Affairs, that the Indians should be helped not to an unearned income but to the opportunity of working for their own livelihood. Nevertheless, if the Indians used every acre of their land themselves and stopped renting altogether, they yet would not have enough land to support themselves at an adequate standard.

Of course, even with the inadequacy of the Indians' resources, good land management exerts a helpful influence. On all but a few reservations we have reduced the amount of livestock somewhere nearly to the carrying capacity of the range. Water developments, increased use of deferred and rotation grazing, better salting, are all tending to make go further what range lands the Indians do possess. We have virtually stopped destructive logging. Forest fires during the past four years have been brought under fairly satisfactory control. Improved farming practice is preventing much of the previous deterioration of Indian agricultural soil. Emergency Conservation, Public Works, and Soil Conservation funds have given the Indians not only an added income but have also helped to conserve their lands. Nevertheless, with all of the improved technique and with all of the work relief funds, the Indian land is still so insufficient that either the Indians will live close to a starvation level or the land will deteriorate.

To any one interested in the welfare of the Indians, the natural question arises: "Why not have the government buy them more land, since the government will have to support them anyway, if they cannot support themselves? Won't the purchase of lands adequate for the earning of their own livelihood be the best way the government can solve the Indian problem, as well as being most satisfactory to the morale of the Indians, because people as a whole are better off socially when working for a living than when living on a dole?"

The answer to these questions seems to be a vociferous *yes*. Nevertheless, there is a hitch. Splendid as this solution may be for the Indians and for the perpetuation of their resources, the land to be bought must be taken from someone. In all that vast domain between the 100th meridian and the Cascade-Sierra Divide, there are already at least half again as many livestock as the range will stand. Yet, except for some large companies, the amount of livestock is only enough to earn a most modest livelihood for the ranchers of that region.

Consequently, the problem of giving the Indians enough land is inextricably entangled with the problem of giving the white people of the interior West the opportunity for a reasonable standard of living. The ecology of most Indian Reservations is not only a zoological and botanical problem, but it is also fundamentally influenced by the dominant economic problem of how to make all of the United States yield all of its citizens a reasonable standard of living.

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A SURVEY OF SOIL TEMPERATURES IN THE CHICAGO AREA

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INTRODUCTION

The sand dunes in Indiana at the southern end of Lake Michigan offer a series of plant and animal communities which have been the object of much ecological study since Cowles' (1899, 1901) analysis of the plant succession and Shelford's ('07, '13) description of the faunal succession.

Quantitative data on various physical factors of these communities have been collected by several workers. Soil temperatures, however, have remained uninvestigated and, at the suggestion of Dr. W. C. Allee, temperature recordings were taken in conjunction with studies of solar ultraviolet and of the local distribution of Orthoptera.

METHODS

Over most of the period of observation ordinary soil thermometers (Fahrenheit) were used. The records taken with these instruments have been translated to the centigrade scale. Air temperatures and many soil surface temperatures were measured with centigrade thermometers of the usual laboratory type.

Since all the data so obtained represent diurnal conditions only, two Friez soil thermographs, which had been appropriately checked, were put into use on July 30, 1935, and operated until February 29, 1936. As only two of these instruments were available they were moved from one associates to another from week to week. One of the thermographs was arranged to record soil temperature at the surface, the other at a depth of six inches. Due to the construction of the instruments the "surface" recordings represent conditions to a depth of one inch, the diameter of the bulb. In shaded sites the thermograph agreed within a degree or less with thermometer readings of surface temperatures.

The total period of observations extended from January 1934 to February 1936. Where time is indicated Central Standard is to be understood. The localities at which observations were made include sites in the sand dunes and forests along the southern shore of Lake Michigan from Millers, Indiana, to Lakeside, Michigan. The thermograph records were taken at Wickliffe, Indiana, about thirty-five miles south and east of Chicago. Some recordings were also made on the prairie west of Chicago, in the oak forests on clay at Palos Park, Illinois, and in the maple climax on clay at Joliet, Illinois.

Air temperature records of the meteorological station at the University of Chicago were used as a basis for comparison of the thermograph recordings in the different associates. A check of air temperatures (shade) taken in the field against meteorological station records showed a maximum deviation of 4° C. and an average deviation of 1.1° C.

SOIL TEMPERATURE DATA

1. *Maximum Temperatures.* The upper beach and foredune present a surface of almost pure sand fully exposed to solar radiation. The growths of *Ammophila* give a slight amount of shade of shifting pattern but modify soil temperatures but little. It has been found that where areas of sand are exposed to solar radiation surface temperatures on clear summer days reach or surpass 50° C. Figures 1 and 2 show the course of soil temperatures in exposed and in shaded areas. From these figures it is evident that surface, and to a considerable degree subterranean temperatures, follow in their trend the course of solar radiation rather than air temperatures.

O. Park ('31) states that only 16 per cent of the surface area in the complex designated poplar associates is actually shaded at any one time. Much of this shaded portion is subjected during the course of the day to prolonged and intense solar radiation due to the wide spacing of the trees. Thermograph records show a rise in surface temperature

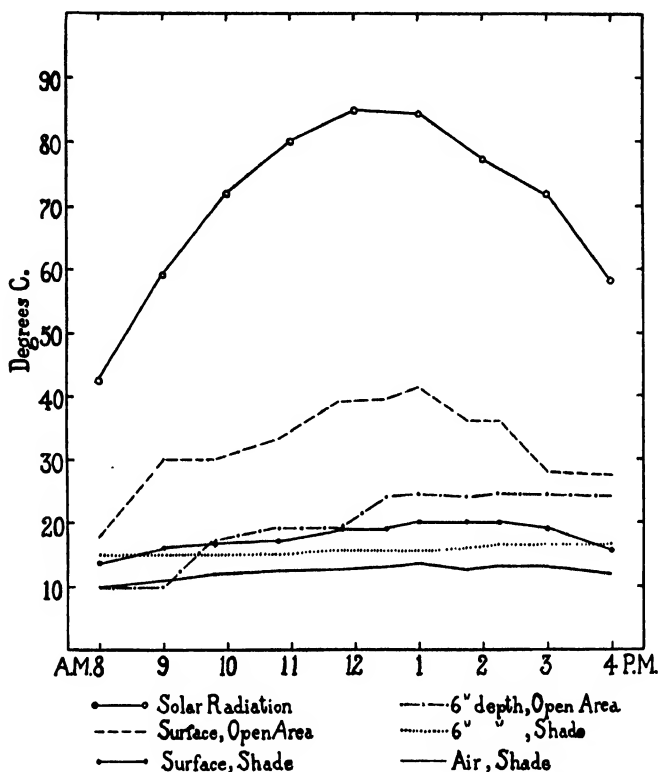


FIG. 1. The relation between soil temperatures, air temperature and solar radiation in the pine associates on May 24, 1935. The points on the curve of solar radiation represent hourly sums. For this curve the scale should be read as G.-cal./cm.²/min. Solar radiation from pyrheliometer records of University of Chicago. Cf. figure 2.

from 29° C. to 46° C. within two hours following the incidence of full solar intensities. Areas in continuous shade are very small. Soil temperatures in such sites are comparable to those prevalent in the oak forest. Except for these areas of small extent the poplar associates presents essentially the same conditions of soil temperature as prevail on the foredune.

The pine community resembles in these respects the poplar more than it does the later associates. According to O. Park ('31) the amount of ground area in shade comprises only 22 per cent of the total area. In the exposed portions of the pine associates soil temperatures equal those of the foredune. Here, as in the poplar community, the spacing and contour of the trees is such that the areas in shade are reduced to a minimum at the time of greatest intensity of solar radiation.

Quite commonly surface temperatures in these three communities reach 45° C. by 9:00 or 10:00 A.M. and by 1:00 or 2:00 P.M. have surpassed 55° C. Soil surface tem-

peratures of 50° C. or above have been recorded in May, June, July and August. The absolute maximum recorded was 64° C. in the pine dune associates on July 24, 1934, at 1:00 P.M. when the air temperature in the shade was 40.5° C. and the surface temperature in shade was 40° C. Soil surface temperatures of 40–46° C. have been recorded in the growths of *Arctostaphylos* in the pine associates.

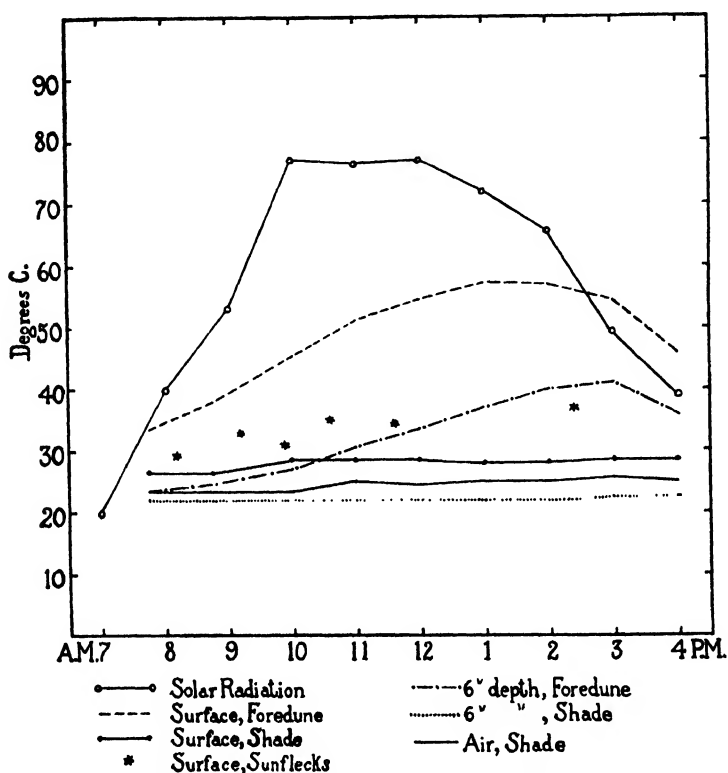


FIG. 2. The relation of soil temperatures on the foredune and in the oak associate with air temperature and solar radiation, July 29, 1935. The points on the curve of solar radiation represent hourly sums. For this curve the scale should be read as G.-cal. cm.²/min. Solar radiation from pyrliometer records of University of Chicago.

The exposed areas in the oak associates comprise only 35 per cent of the total area and the total amount of sunlight penetrating to the forest floor is less than one-half the incident on exposed sites (O. Park, '31). There is a corresponding reduction in maximum soil temperatures.

During late April and even into May before full foliage has been assumed greater part of the forest floor is subjected to intense solar radiation. As a consequence surface temperatures rise above those of the air. Due to the mold and leaves covering the earth the maximum temperatures attained here do not equal those reached in the open associates. The maximum of the records at this season is 25° C. on May 7, 1934 the air temperature was 15° C. At the same time the soil surface in an unshaded area in the pines was 36° C. Before the incidence of greatest solar intensities and

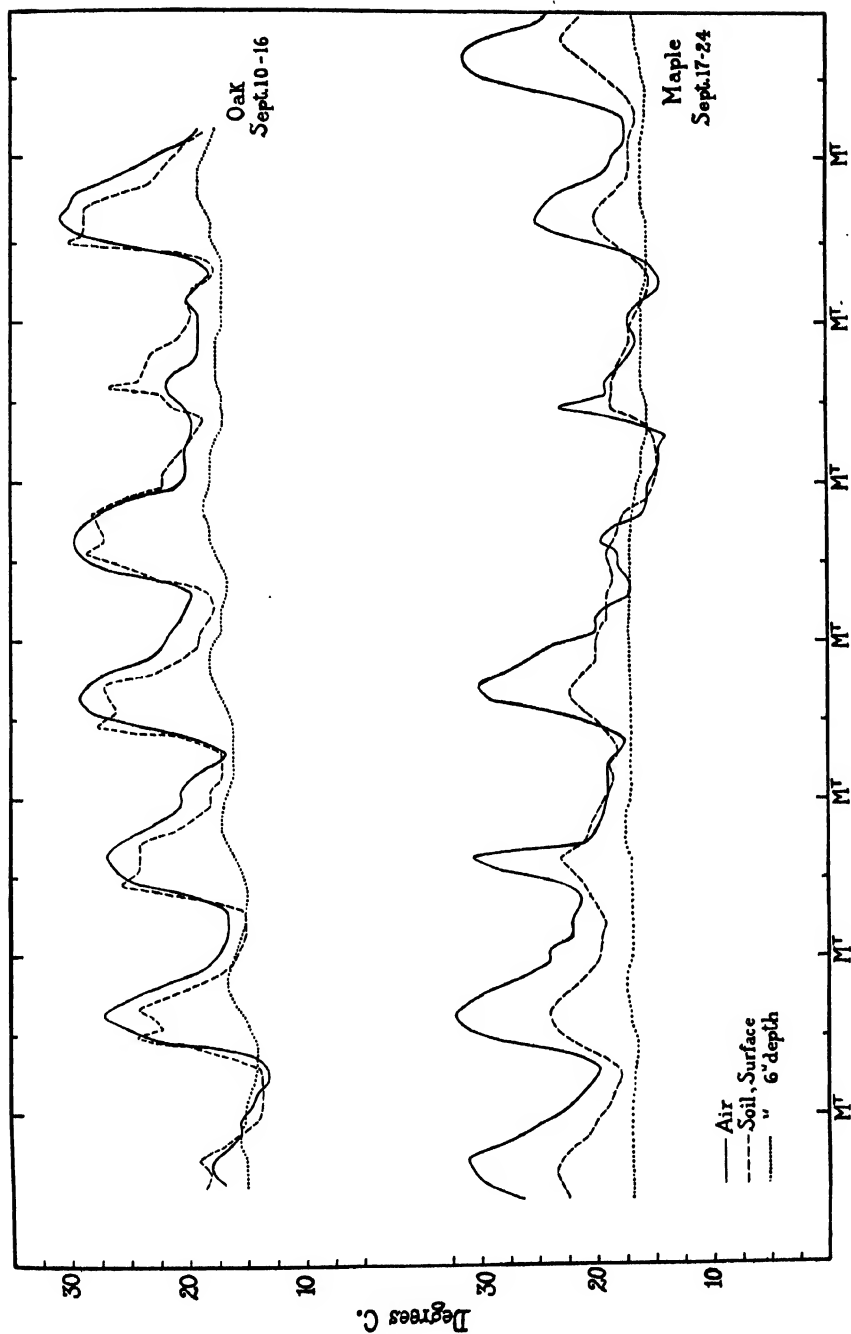


FIG. 3. Trend of soil temperatures in the oak and climax associates. Air temperatures from meteorological records of the University of Chicago. Note that soil surface temperature in the oak associates follows air temperature more closely than does that of the climax.

temperatures the leaf canopy of the oak forest is fully developed and has tremendous effect in the maintenance of moderate soil temperatures. Figure 2 illustrates the course of diurnal soil temperatures in a well shaded site in the oak forest contrasted with that of an area fully exposed to solar radiation. There is variation in soil temperature from spot to spot in the oak forest due to sunflecks. The sunfleck pattern is, however, a rapidly shifting one so that no portion of the forest floor remains long in high intensities of sunlight. Figure 2 shows random measurements of surface temperatures in sunflecks in the oak associates.

The definitive climax forest presents a floor in almost continuous shade during the period of foliage. The heavy covering of leaf mold keeps soil temperatures low in the spring before the leaf canopy has developed. The highest surface temperature recorded in this type of forest was 24° C. on August 19, 1934, when the air temperature was 30.5° C. This was repeated on September 17 and 18, 1935, with air temperature at 31.5° C. It is to be noted that in the climax forest soil temperatures are somewhat lower than air temperatures during the day while in the oak forest the two are about equal. This applies, of course, only to the warm period of the year (fig. 3). In the oak forest soil surface temperatures may rise above air temperatures on cool, clear days due to insolation.

Measurements made on clay soil west of Chicago indicate that for sites of equal exposure soil surface temperatures are comparable to those of sand. The maximum recorded on dry prairie was 57° C., which approximates the 64° C. for sand, while in the oak-hickory forest on clay a maximum surface temperature of 35° C. has been measured, which agrees closely with the maximum of 38° C. for the oak forest on sand. Table I gives the average maxima in the different associates as actually measured.

TABLE I. *Mean monthly maximum soil temperatures (degrees C.) in the associates of the plant succession on sand in the Chicago area*

	Foredune *		Poplar (Shade)		Pine (Shade)		Oak (Shade)		Climax	
	Surf.	2-6" depth	Surf.	2-6" depth	Surf.	2-6" depth	Surf.	2-6" depth	Surf.	2-6" depth
Jan.				-1.0		-1.0		.7		1.9
Feb.	1.2	-1.0	-1.2	-1.0	-1.0	-1.0	-2.0	-1.0	-2.0	-1.5
March										
April	32.0	21.0			6.0	6.0	16.0	9.0		
May	38.5	24.0			21.3	13.8	18.5	14.0	14.0	11.0
June	46.0	29.5	25.0	23.0			23.0	16.5	16.0	13.5
July	47.0	36.0			32.0	28.0	24.5	22.0	19.0	16.0
Aug.	54.0	33.5	25.3	22.9	37.0	30.0	23.0	20.0	22.0	19.0
Sept.			20.4	16.4	22.6	17.2	26.0	17.5	21.6	16.8
Oct.			17.9	13.1	19.5	13.0			16.3	
Nov.			17.5	13.8	15.0	14.8	10.6	12.3		

* May be taken as indicative of soil temperatures over 80-85 per cent of the poplar and pine associates.

Whether these data are strictly representative of conditions is open to some question as in no case do they represent records of more than twelve days and in many instances only three or four. Table 2 gives the approximate annual maximum soil temperatures in the various associates.

2. *Minimum Temperatures.* From the thermograph records for August, September and October it appears that the daily minimum surface temperatures in all the associates are about equal to daily minimum air temperatures (fig. 3). At a depth of six inches

the fluctuation is less marked during the day but the daily minima are not greatly different from those of the surface. In the autumn there is, as would be expected, a period when soil temperatures at this depth are above those of the air.

TABLE II. *Approximate yearly maximum and minimum soil temperatures in the various associates of the dune succession*

	Maximum ° C.		Minimum ° C.	
	Surface	6" depth	Surface	2" depth
Foredune	64	45	—	(-3.5)
Poplar	64	45	—	-3.5
Pine	64	45	—	(-3.5)
Oak	38	26	—	(-3.0)
Climax	24	18	—	-1.5

Actual data as to the annual minima are not at hand except for the poplar and climax associates. At a depth of two inches the minimum soil temperature recorded in the former was -3.5° C. and in the latter -1.5° C. The annual minimum air temperature was -28° C. The ground at the time the soil recordings were made was covered by several inches of snow; hence the thermograph bulbs received this further insulation. These records probably represent very nearly the lowest soil temperatures as the air temperature cited has been equaled only twice in the history of the meteorological stations in Chicago and very low air temperatures here are usually preceded by considerable falls of snow. This supposition is supported by the data of Holmquist ('31) who records a minimum of -5.3° C. under leaves.

Table II gives approximations of the annual minimum temperatures in the different associates of the plant succession.

DISCUSSION

The records of soil temperatures on the sand dunes at the southern end of Lake Michigan show maximum surface temperatures about equal to those given by Chapman, Mickel and Parker ('26) for the dunes near Minneapolis. They recorded a maximum of 56° C. and found that this temperature quickly killed insects which were not adapted in some way to the conditions on the dunes.

Soil temperature conditions on the open sand are essentially those of a desert environment as regards maxima. Sinclair ('22) reports surface temperatures of 71.5° C. in the desert at Tucson, Arizona. Taylor and Burns ('24) recorded 68° C. on the soil surface in Egypt. Kashkarov and Kurbatov ('30) measured surface temperatures of 58.5° C. in the Kara-Kum Desert in April. They have well remarked that in such habitats, "the average climate does not exist at all."

Mosauer ('36) gives records of 62° C. for the California desert and found that desert reptiles were quickly killed when confined to sand at such temperature. It appears, from the experience of Mosauer and of Chapman, Mickel and Parker, that the ability of some animals to survive in these environments is due more to structure and behavior which enable them to escape the high extremes than to ability to actually endure the temperature.

As noted before, there is some question as to how accurately the records presented here typify soil temperature conditions throughout the year. For the months of April, May, June and July, measurements were made on the clearest days of the month as shown by pyrhelimeter recordings of the meteorological station at the University of Chicago. The records of temperatures on the foredune in August are also confined to clear days.

If, however, we assume that the data are indicative of conditions in the different associes it appears that high surface temperatures in the early associes may be a critical factor in the exclusion of many species of animals. On the other hand the higher soil temperatures in the foredune, poplar and pine associes in the spring (table I) may be essential to the development of certain species, which, for this reason, are restricted to open sites in the sand.

Annual minimum soil temperatures as determined at a depth of two inches suggest nothing of ecological significance. The lowest record at this depth is -3.5° C. in the poplar associes, which is not greatly different from the minimum of -1.5° recorded for the climax forest. Both of these minima are well within the limits of toleration of hibernating animals.

SUMMARY

1. Soil surface temperatures in the foredune, poplar and pine associes are characterized by high extremes on clear summer days; the maximum measured was 64° C. In very limited areas in the poplar and pine associes which are in continuous shade soil temperatures are about equal to those of the oak forest.

2. The soil of the oak forest has maximum temperatures much below those of the earlier stages of the succession; the maximum actually determined was 38° C.

3. Soil temperatures in the climax forest apparently do not surpass 24° C. and are characterized by less daily fluctuation than are those of the oak forest. At a depth of six inches soil temperatures may remain practically constant for a week or more.

4. Winter minimum soil temperatures are very nearly the same throughout the succession. The difference between the minimum of -3.5° recorded in the poplar associes and of -1.5° recorded in the climax forest does not appear to be of any ecological significance.

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BURIED FORESTS IN BOGS OF SOUTHWESTERN IRELAND

In parts of Ireland buried wood is frequently found in digging peat for fuel. As peat is the principal fuel on account of the scarcity of forests and expense of coal, a great deal of peat is dug, and a great deal of buried wood with some of it. One frequently sees large piles of this wood, and sometimes even fences made of the stumps.

Gougane Barra is a lake lying in a glacial cirque in the mountains of southwestern Ireland, and is the headwaters of the Lee River. The lake is justly famous for the wild and rugged beauty of its setting.

On one side of the lake is a bog, partly separated from the lake by a low rocky ridge which probably favored the formation of the bog. A trench for extracting peat has been dug in the bog down to the water table, at a depth of about 5 feet. A good deal of buried wood has been dug out and can easily be examined; and the trench affords an excellent cross section showing the buried forest in place about 30 inches above the water level and overlain by about another 30 inches of fibrous peat, which looks as if it had been formed by sphagnum.

The tree stumps are of Scotch pine (*Pinus sylvestris*) as in other bogs of southwestern Ireland. Many have the bark intact, and the wood, when cut, is as sound as in a board fresh from the saw.

Pieces of peat were found which looked like sections lifted from the forest floor of a living forest. There were twigs, mostly of birch, and some of pine, and even the fibrous feeding rootlets. Mosses seem to have formed an important part of the forest floor, but the determination of these would need microscopic examination.

It is not difficult to picture this forest. It was composed of Scotch pine, with an admixture of birch, probably like forests on bogs in Sweden to-day. The pines, from the shape of the stumps, must have been short and gnarled, showing unfavorable growing conditions.

The evidence of fire is unmistakable in a fire-scorched trunk and twigs of charcoal. This is in spite of the present view that evidence of fire in the buried forests is no longer valid. Nevertheless the fact that there were fires does not mean that these forests were destroyed by fire. Under the climate which must have prevailed to permit the existence of Scotch pine forests on bogs, it would be only natural to have occasional fires set either by lightning or by man. The agency of man is not improbable, as the existence of a high civilization in Ireland as far back as 1500 B.C. is shown by gold ornaments of about that date which exhibit extraordinarily skilled workmanship.

The most probable cause of the disappearance of these bog forests is a change of climate to more humid conditions which favored the growth of sphagnum that overwhelmed the forests. One pine stump was seen in place in the trench which looked as if it had put out roots at a higher level to keep above the ever deepening sphagnum. It has been suggested that the change from Sub-boreal to Atlantic climate, around 10,000 B.C., brought on the end of these forests by increasing moisture. This period would correspond in time approximately with the period of slight increase of the northern coniferous element which Fuller found in the pollen record of the Lake Michigan region.¹ Possibly postglacial time was cooler and moister than the preceding period on both sides of the Atlantic Ocean.

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¹ Fuller, G. D. 1935. Postglacial vegetation of the Lake Michigan region. *Ecology* 16: 473-487.

HYDRA AMERICANA IN OKLAHOMA¹

Hyman ('29) described *Hydra americana* as a new species and gave Chicago and vicinity as its type locality. Its habitat was given as "attached to vegetation in ponds and lagoons, and old streams." It is the purpose of this note to report the collection of this hydra in Oklahoma and to note its occurrence in a habitat somewhat different from that described by Hyman.

The animals were found April 10, 1936, in a small stream near Norman, Cleveland Co., Okla. Most of them were attached to the under side of fallen cottonwood (*Populus deltoides*) leaves although some occurred on stones. The water was but a few inches deep and flowing moderately. On May 23, 1936, one of us (Bragg) also collected this species among densely growing algae in quiet water in a small lake near Norman.

The specimens from the stream were budding profusely when collected. Within two days, many of them became sexual but only females were found. The animals agreed with Hyman's description and figures of this species except that the ovarian theca was not observed.

Hyman ('31) knew of no records of hydras from flowing water in streams. Elsewhere (Trowbridge, Bragg and Self, '36) we have reported *H. littoralis* Hyman from such a situation in southern Oklahoma. It therefore appears that in Oklahoma, at least, two species of *Hydra* are adapted for life in flowing water. It is true that the stream in which *H. americana* was found was not flowing fast; but it should be remembered that after the sudden rains which sometimes occur in this region, this little stream becomes a raging torrent. If the hydras are not adapted for life in flowing water, it is difficult to understand how they maintain themselves in the stream during this time.

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EVIDENCES OF ANCIENT OAK OPENINGS IN SOUTHERN MICHIGAN

Southern Michigan was pioneered by a New England influx following the opening of the Erie Canal. Oak openings, before this settlement, were apparently of irregular occurrence in the middle and eastern half of the southern part of the state. The original vegetation has now been so greatly changed by farming that evidence of oak openings must be sought indirectly.

My family settled in Blackman Township, Jackson County, in 1829. Part of the lands then cleared still remain in possession of the family. On one portion of the dark and heavy clay-loam, circular areas of yellowish-brown appear in the freshly plowed and harrowed ground. These circles are about sixty feet in diameter and astonishingly evenly spaced, averaging perhaps a hundred feet from center to center. This unusual phe-

¹ Contributions of the Zoological Laboratories of the University of Oklahoma, No. 156.

nomenon suggests at once the speculation that this is the site of a former oak opening, the trees themselves gone a century ago yet leaving the interpretative evidence of their ancient stand by yellow circles in the dark soil matrix. It would seem unusual for soil color to change so positively in the life of even a tree, but no other explanation appears.

Fifteen miles southeast, south of my home town of Grass Lake, a number of giant white oaks, *Quercus alba*, grow on the sands and gravels of an esker. Their limbs are gnarled and spreading in full evidence that they developed in the open although the present finds an understory predominately *Populus*. No definite age can be assigned without increment borings or cutting. Yet by analogy, they should be at least a hundred and fifty years old. If this be true, here still lives an ancient oak opening now intergrown with youthful competitors.

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HOW SELECTIVE IS THE HABITAT OF THE POISONOUS *ASTRAGALUS HYLOPHILUS*?

In a recent note¹ Beath states that the poisonous but selenium-free *Astragalus hylophilus*² is restricted to aspen, aspen-pine or pine woodlands and to soils derived from the Bishop or Hanna conglomerates. His statement refers to south-central and south-western Wyoming. Plant collections which I have made in the Uinta Basin of north-eastern Utah in connection with certain phytogeographic studies of that area show that Beath's conclusions are not applicable to northeastern Utah, a region separated from the area which he studied only by the Uinta Mountains. These collections, now in the Carnegie Museum Herbarium, include the five following Utah localities for the "Timber milk vetch," *Astragalus hylophilus*: (1) In mixed aspen-pine woods, on glacial moraine overlying Mississippian strata and derived from pre-Cambrian quartzite, south of Moon Lake, north-central Duchesne County, 8100 ft., June 30, 1931, *Graham 6440*; (2) in sagebrush, on carboniferous limestone, near Little Lake, 15 miles north of Vernal, north-central Uintah County, 8300 ft., June 23, 1933, *Graham 8242*; (3) in sagebrush, on Green River (Eocene) shale, below Mud Springs, 2 miles west of Indian Canyon Pass, 10 miles northeast of Castle Gate, southwestern Duchesne County, 8800 ft., June 29, 1935, *Graham 9480*; (4) in aspen woodland, on Green River (Eocene) shale, upper Rock Creek, near Willow Springs, 10 miles east of Sunnyside, eastern Carbon County, 9200 ft., July 11, 1935, *Graham 9589*; (5) in aspen woodland, on Green River (Eocene) shale, head of Hill Creek, northwestern Grand County, 8500 ft., July 31, 1935, *Graham 9946*.³

From the above data it is evident that *Astragalus hylophilus* is not everywhere confined (1) to aspen, aspen-pine, or pine woodlands, but may also occur in open sagebrush areas, nor (2) to conglomeratic soils, but may also occur on glacial moraine derived from pre-Cambrian quartzite, Eocene shale, and Paleozoic limestone. All of the specimens cited were in flower when collected and there were also maturing legumes on the number collected at the head of Hill Creek. At this locality a sheep herder complained about losing a number of sheep from a herd which was grazing there at the time. He

¹ Beath, O. A. 1936. Selective habitat of the poisonous *Astragalus hylophilus* (Rydb.) A. Nels. *Ecology* 17: 692-694.

² *Astragalus hylophilus* (Rydb.) A. Nels., *Homalobus hylophilus* Rydb.

³ The determinations of the plant specimens cited were verified by Prof. Ivar Tidestrom of the Catholic University of America, a specialist on the genus *Astragalus*; the geological data have been confirmed by Mr. J. LeRoy Kay of the Carnegie Museum, who has studied the geology of the Uinta Basin for many years.

pointed out *Astragalus hylophilus* as the cause and was convinced that this plant was killing his animals. So the species seems to lose none of its poisonous properties in the Uinta Basin, even when growing on soils which are not derived from conglomerates.

It would, therefore seem that in looking for factors which determine the occurrence of the stock-poisoning *Astragalus hylophilus* we shall have to consider more than soils and plant associations. What this will be it is difficult to say, but it is interesting that the five localities cited above occur within comparatively narrow altitudinal limits, namely between 8100 and 9200 feet. In such arid regions as the Uinta Basin, climatic factors vary greatly with altitude, and perhaps such elements as moisture, temperature, evaporation, etc. are the limiting factors in the occurrence of this species after all. Unfortunately, appropriate climatic data for the Uinta Basin localities cited are not available.

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EXPERIMENTAL POPULATIONS OF MICROSCOPIC ORGANISMS

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I

In an attempt to discuss the problem of experimental populations, a living and rapidly developing chapter of experimental ecology, it is perhaps best to concentrate on the consideration of all the possibilities, and particularly of all the limitations inherent in this new biological *Wissenschaftszweig*. The origin of this line of investigations appears to be deeply rooted in the quite natural desire of human beings to master the laws governing the structure and activity of the biosphere in which they live, in order to modify it and to adapt it to their own ends. The problem of the biosphere, of that specific envelope of our planet saturated with populations of living beings, is at present attacked from at least three different angles. Firstly, in biocoenology by describing, qualitatively and quantitatively, associations of living organisms under field conditions. Secondly, in biological geochemistry by analyzing the chemical consequences of activities of these populations. And thirdly, perhaps the most recent line tries to discover general principles of organization in these population systems by means of experimental analysis.

Various opinions concerning the rôle of experimentation in biocoenology are extremely contradictory, and one may still meet active scepticism denying any significant rôle of experimentation in this particular field. "The data," as it is often said, "obtained in the laboratory under 'unnatural' conditions are of extremely little value and sometimes are even misleading." On the other hand, to overrate the potentialities of the experimental method would perhaps be equally dangerous. It therefore appears best to mention them briefly.

It is interesting to find late in the past century an analogous discussion concerning the rôle of experimentation in zoölogy. We meet O. Hertwig's claim to a specific restriction of application of experimental method by physics

and chemistry, and its uselessness in biology: "*das Experiment habe seine eigentliche Bedeutung im Gebiete des Anorganischen. Da die anorganischen Körper verhältnissmäßig unveränderlich seien, so müssen sie durch den Menschen gezwungen werden, sich zu verändern, und erst dadurch werden sie der kausalen Forschung zugänglich gemacht.*" We meet further Driesch's energetic and clear cut reply in defence of experimentation in biology: "*das Experiment wird nicht allgemein Veränderungen herbeiführen, sondern will Veränderungen (Vorgänge) nach Belieben isolieren oder variieren. . . . Ganz dasselbe, was den Wert des Versuchs in den anorganischen Disziplinen ausmacht, trifft nun auch vom biologischen Versuch zu.*"

The rôle of experimental method in biology is now generally recognized, and by extending it to the study of biological "associations" we appear to be making a perfectly logical step of lowering it to the next hierarchical level. At the same time there appears to be a certain specificity in that particular level, which is at least worthy of some attention. In the study of an individual organism it is usually relatively easy to distinguish between inherent organismal properties which are due to a specific order of matter which makes it living, and relatively secondary variations in these properties which are associated with differences in environmental conditions. Putting it in another way, the living matter appears to be rigorously organized, and the very existence of this organization admits of no doubt. At the same time the degree of organization of "associations" of living beings is of an entirely different order of magnitude. The principles inherent in these associations as such (*e.g.* regulation in composition, etc.) are not always clear owing to a relatively more efficient rôle of the environmental situation. The field studies have therefore the advantage of showing us the exact behavior of such-and-such an association under such-and-such a set of environmental conditions, which is sometimes of immediate use for practice. At the same time no claim can be made to an adequate theoretical understanding of the principles of its organization by field observations alone, and definite room is therefore left for application of the experimental method.

The position of experiment in biocoenology has much in common with the rôle which relatively simple physical facts, obtained through experiment, play in the science of meteorology. It is certainly true that at the bottom of all weather variations lie some definite physical facts, which have been, and surely will be productively studied under simplified laboratory conditions. It is equally true that an adequate understanding of some weather phenomena could never have been attained without laborious experimental work of this sort, and nobody will ever doubt of its importance. At the same time an attempt to forecast weather on the basis of such laboratory investigations *alone* will scarcely meet with any approbation.

To sum all this up: although an individual organism is either *somewhat* modified or perfectly eliminated by environment, a biocoenosis is really *made* under rigorous control of environment. Those features which are specific

for a developing biocoenosis as such and hold true under any set of conditions are therefore not very evident at first, but they undoubtedly exist and are worthy of experimental analysis. It is therefore the object of experimental study of populations to find out some very general principles underlying the organization of biological associations.

II

Populations of *microscopic* organisms appear to be particularly suitable for experimental work because (1) it is very inexpensive to undertake all the manipulations required, and (2) these manipulations can be accomplished in a very short while. My early studies on populations were conducted in field conditions on various grasshoppers about ten years ago; they were continued in the laboratory on *Drosophila* cultures in milk bottles. But finally I found populations of various yeasts and infusoria to be extremely suitable for work of this sort. To the list of our laboratory animals have recently also been added mites inhabiting wheat flour, semolina and some other substrates. These are extremely small and must be counted under a microscope; in this way we are right to rank them among populations of microscopic organisms.

In search of some general principles governing the structure of associations I have first used the simplest possible method, that of analysis into elementary constituting processes. An attempt was made to investigate, under carefully controlled laboratory conditions, the trend of elementary processes of the struggle for existence between various species and the consequences to which they lead. Complete information concerning all details could best be obtained from my books on the subject (Gause, '34; '35) and all additional information from three papers (Gause and Witt, '35; Gause, '36; Gause, Smaragdova and Witt, '36).

A mixed population in the test-tube was first made of the two species of yeast, and then of the two infusoria, *Paramecium caudatum* and *Paramecium aurelia*, presenting equal requirements regarding the kind of food and mode of its consumption or, in other terms, occupying identical "ecological niches" in the microcosm under investigation. The outcome of such an experiment was always identical and clear-cut: only one species, the better adapted for living under given conditions, was finally left in the population, which in this way had become *pure*. It is also interesting that it was possible to calculate *in advance* which one of the two species would be left, from an equation of growth for such a mixed population.

In so far as a mention has just been made of mathematical equations it seems best to say a few words concerning the rôle of this method in the study of experimental populations. It is sometimes argued, and not without sound reason, that when a mathematician tries to introduce all even secondary details specific for some experimental population into his theoretical calculations, he can scarcely get conclusions of any permanent value for understand-

ing real animal life in the field. The conditions, and consequently the conclusions, will surely be different in the field. This reasoning originates from a real difficulty of recognizing some underlying fundamental principles of associations of organisms in the complex of their details. Mathematics will be of value in the study of populations which will seek principles and not merely unimportant details.

The danger of the neglect of details is scarcely to be emphasized, for it is too evident that any separation of the "meanly net" from its "gist" is only possible when the net is carefully and definitely understood. But what is the kind of "gist" that a mathematician could help us to get out "net"? Since we are dealing with quantities, with numbers of animals, we will be supplied with qualitatively different *types* of variations of these numbers. We will be exhaustively told how different types of interaction between organisms in associations lead to different types of the steady states of these systems: either to continuous periodic variations in numbers, or to a continuous stable mixed population capable of autoregulation, etc. Using technical terms of mathematicians, the principles we are looking for are nothing but types of qualitative solutions of differential equations for various population systems.

The first such principle we have heretofore observed experimentally and accounted for theoretically, both in infusoria and in yeasts, is that the steady state of a mixed population consisting of two species occupying an identical "ecological niche" will be the pure population of one of them, of the one better adapted for the particular set of conditions. The second type of the steady state we are now going to discuss appears to be particularly interesting from the viewpoint of a field naturalist. Certain suggestions concerning its nature were at first given theoretically by Lotka, Winsor and myself, and since then it has been experimentally demonstrated for two population systems in infusoria. If we take a test-tube containing a mixed diet consisting of bacteria and yeast, and populate it with the two species of infusoria, *Paramecium aurelia* and *Paramecium bursaria*, the first of which will prefer bacteria and the second yeast sediment on the bottom, we will apparently have to deal with a mixed population of two species occupying two different ecological niches contained within the same microcosm. Both species can certainly eat each kind of diet, but each one of them is particularly well-adapted to its own mode of nutrition. The outcome of such an experiment shows the existence of a specific steady state, the stabilization of a steady mixed population of both species. Two species occupying different ecological niches in the habitat continue to live together indefinitely in essentially stable equilibrium, in which each one occupies the niche where it is more efficient. This appears to be the second principle of biological association yielded by experimentation and accounted for by theory.

The theoretical interest of this principle lies also perhaps in the fact that it gives a satisfactory account of regulation in association, on a very primi-

tive level of its organization. In fact, not any but only a certain *definite* combination between the two species possesses the property of maintaining stability. Any deviation from it will automatically, owing to continuous process of competition, lead to re-establishment of the steady state.

All this appears to hold true, as far as the mixed population of *Paramecium aurelia* and *Paramecium bursaria* is concerned. Certain significant differences have, however, been found in cases of *Paramecium caudatum* and *Paramecium bursaria*. The re-establishment of a disturbed equilibrium did regularly take place when *Paramecium caudatum* was in excess, but ceased to operate in case of excessive increase of *Paramecium bursaria*. Subsequent experimental analysis has shown that this is due to a specific sensitivity of *Paramecium caudatum* to the waste products excreted by *Paramecium bursaria*; the former is in this way unable to increase in dense populations of the latter. What is essential in these data is perhaps the realization of relative parts played by a more general principle of automatic regulation and of a more special disturbance if this regulation changes under some conditions due to specific biological particularities of experimental animals. An interplay of these two parts is responsible for the design of complicated natural phenomena as we see them.

III

Another group of elementary processes of interaction between species in associations, that of *direct* struggle for existence, should perhaps be only briefly mentioned. It was at first observed on infusoria, and later on mites inhabiting both semoletta and wheat flour, that an interaction between predators and prey in a closed habitat can lead either to extinction of both in case of sufficient voracity of the former, or to oscillation in numbers under conditions of continuous immigrations of predators and prey from the outside. An essentially different behavior was observed in a less voracious system consisting of *Paramecium* devouring yeast cells, where continuous variations in numbers of both species were demonstrated under some conditions. Certain advances in both experimental technics and theory enabled us to conclude that this type of variation is essentially due to two factors: (1) the impossibility for infusoria to consume yeast cells to the very end with the resulting threshold of consumption, and (2) a peculiar relation between the increase of predators and the density of prey, that give to these variations their specific shape.

The two mentioned types are nothing but elements that participate in the complicated design of real natural events.

IV

Although analysis into constituting entities almost always precedes the study of coordination of these entities into units of higher order, it seems

reasonable to ask at this stage what we can hope to obtain from experimental populations of microscopic organisms for understanding biological associations in their complexity? In this connection we should like to mention some new possibilities that seems to open regarding the very mode of experimentation. If we want to pass from elements subject to laboratory analysis, to an interplay of these elements, something intermediate should evidently be taken between highly complex field biocoenoses and extremely simple laboratory mixed populations. Elements of complexity, if you like, should also be studied in their *relatively simple* form. Some opportunity for this is offered by the study of fouling by various microscopic organisms of glass plates submerged in natural waters. The first such attempt was made by Hentschel in Hamburg in 1916, and a very effective extension of this method is due to several Russian authors. The submerged glass plate begins to be covered by various microscopic organisms in a very orderly way, which steadily grow in number and enter into competition with each other. A stage of a relatively stable mature biocoenosis is finally reached, but it is still subject to continuous alterations in composition due to variations in environmental conditions.

It is perhaps particularly convenient that it is extremely easy to interfere experimentally from the outside with the competition and other relations in this rapidly developing biocoenosis on the glass plate. Some organisms can be easily eliminated with different intensity by a thin needle. In the summers of 1935 and 1936 I used the opportunity of experimentation with such biocoenoses of microscopic organisms on glass plates in a lake near Moscow.

For the beginning of the study of complexity in biological associations, there seem to be at least two problems worthy of experimental attack. These are the principles of regulation and of biocoenotic discontinuity. The first of these was already briefly mentioned in the discussion of elementary constituents, and about the same picture was observed in the study of complexes on glass plates. In one series we had two dominating algae, *Microneis* and *Lyngbia*, that competed for space and later reached a temporary equilibrium. When *Lyngbia* was artificially rarefied in a very considerable proportion, the equilibrium was disturbed, but later on became re-established again owing to competition. The complexity of populations on glass plates is enormous in comparison to that in test tubes, and in the future are expected to exhibit various disturbances of a proper regulation in composition, of the type we have previously described for *Paramecium bursaria*.

The essence of the principle of biocoenotic discontinuity could perhaps be outlined in this way. How, under a continuous gradient of environmental factors that steadily pass from one value to the other, can discontinuous units of structure come into existence, known as associations of living organisms? The data obtained in the field alone are not always entirely satisfactory considering the extreme difficulty of recognizing both the elements of continuity and discontinuity. Some experiments have been recently made by me in which the effect was studied of the continuous alteration in the active reaction

of the medium upon an artificial biocoenosis consisting of nine species of infusoria in the test tube. At early stages of growth the differences between mixed populations (that were at the start identical) appeared to be continuous, and discontinuity in composition was recognized only later in their development. One species, *Holosticha*, was depressed on a part of the environmental scale due to physiological causes, mainly because of its sensitivity to increased concentration of phosphates. In this way it let another species, *Paramecium bursaria*, come in, which was otherwise not admitted due to the biocoenotic reason of the presence of *Holosticha*, being itself relatively insensitive to phosphates. In its turn *Paramecium bursaria* depressed a third species, *Halteria*, and thus we have discontinuity of alteration if the composition of associations as regards the environmental gradient has become steadily established.

In the light of all the data available it is scarcely admissible at this stage to wave experimental study of microscopic populations aside and content oneself only with observations of nature as it stands before us in the field. But neither do we expect to find in the experimental population a universal panacea of all our troubles. What we need are more careful investigations of this sort, out of which in the next decade will perhaps evolve another series of general principles of biological associations.

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A NOTE ON EVAPORATION

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This communication was prompted by the appearance of D. B. Anderson's article "Relative humidity or vapor pressure deficit" in the issue of *ECOLOGY* for April, 1936. Publication of Anderson's article, the theoretical basis of which will not withstand serious criticism, may warrant a re-examination in the pages of the same journal of the dependence of rate of evaporation on physical factors. The discussion leads to a new evaporation equation, approached by modern ways of thinking about the movement of fluids. The equation, while original in its formulation, owes much to earlier, but recent, theoretical discussions, particularly those contained in the literature cited under Nusselt ('30) and Büttner ('34). My aim is not only to show the inadequacy of the view of evaporation represented by Anderson's article, but also to present a sequence of reasoning regarding the process that is in tolerable accord with current physical theory.

Anderson's fundamental principle, stated explicitly in many discussions of evaporation to be found in botanical literature, is that rate of evaporation is proportional to vapor pressure deficit of the air into which evaporation is taking place. It will be shown presently that this principle is untenable. How it attained the popularity it seems to enjoy in botanical circles is a question my limited acquaintance with the pertinent literature will not permit me to pursue in detail. One possible line of derivation may, however, be cited. In a short article published in 1917, Livingston (p. 172) defined vapor pressure deficit as the difference between saturation vapor pressure at a free water surface and the vapor pressure obtaining in the air above the surface; and asserted that rate of evaporation, the influence of wind being neglected, is proportional to this difference. Livingston was right in supposing that rate of evaporation is proportional to the difference in vapor pressure thus defined, but unwise in calling it "vapor pressure deficit," which term can be correctly used only for the difference between the maximum possible vapor pressure in space at a given temperature and the vapor pressure actually obtaining there. Stated in a convenient algebraic notation, E denoting vapor pressure at saturation, e actual vapor pressure, and the subscripts 0 and 1 position at an evaporating surface and in the air respectively, Livingston was correct in asserting the proportionality of rate of evaporation to $(E_0 - e_1)$, but injudicious in calling that difference "vapor pressure deficit," which expression should be used and is used exclusively for the difference $(E_1 - e_1)$. Livingston warned his readers against the confusion that might arise from the assumption that $E_0 = E_1$,

which is true only if the temperatures of the evaporating surface and the air above it are equal. But in the latter part of his article he set the bad example of using $(E_1 - e_1)$ as if it were identical with $(E_0 - e_1)$.

Whether or not this article of Livingston's is the source of the fallacy, not long afterward one of his disciples (Johnston, '19) attempted to find a correlation between rate of evaporation from porous-cup atmometers and vapor pressure deficit of the air, using observations made over a wide range of weather conditions. Johnston cited Livingston's polemic explicitly, but followed example rather than precept. He used $(E_1 - e_1)$ unquestioningly, and accordingly found only a dubious correlation between it and rate of evaporation.

Equality of temperature between evaporating surface and the air above it must be looked upon as a very special condition. It might be attained in the laboratory (though maintaining it would be a delicate procedure, requiring the addition of heat to the evaporating surface from some source other than the air at precisely the rate of loss of latent heat by evaporation), but in nature it is certainly exceptional. The temperatures of all evaporating surfaces with which the readers of this journal are concerned—bodies of water, the soil, transpiring leaves, evaporimeters—vary upward and downward, only roughly parallel to the fluctuations in temperature of the air, through ranges that seriously affect rate of evaporation from them.

The principle that rate of evaporation is proportional to vapor pressure deficit of the air would deny, to take an extreme example, that evaporation can take place into saturated air; but one can see evidence that it does take place, from vessels of heated water, from open bodies of water in cold winter weather, from wet roofs and pavements when the sun shines on them. It would insist that evaporation always takes place from a water surface into air that is not saturated; but the accumulation of dew through condensation from unsaturated air, the direct opposite of evaporation, is a matter of the commonest observation. Not the vapor pressure deficit of the air, it is to be insisted, determines whether water molecules pass into or out of a water surface; but, as Livingston correctly argued in the article cited, the difference in concentration of water molecules between the layer of air immediately in contact with the evaporating surface and the air above. If the water surface and the air next to it have a lower temperature than the air above, concentration of water vapor in the air above the surface, though it does not saturate the air at its temperature, may exceed the concentration in the cooler saturated air next to the water surface. If such is the case, as in the growth of dewdrops, water will be deposited from the unsaturated air on the surface of the water. If the gradient of water-vapor concentration is directed away from the water surface into the air, evaporation will take place, but not otherwise. This is an elementary physical principle, with which the doctrine of proportionality of rate of evaporation to vapor pressure deficit of the air is utterly irreconcilable. No formula asserting

such proportionality is to be found in physical and meteorologic literature. This literature abounds in equations that relate rate of evaporation to physical factors, but in all, from the earliest, formulated by Dalton over a century ago, to the latest, the humidity difference used is $(E_0 - e_1)$ or its equivalent.

Vapor pressure deficit is, moreover, not the only meteorologic function to which rate of evaporation is proportional under special conditions. One that is more easily obtained is depression of the wet-bulb temperature. Rate of evaporation is rigorously proportional to wet-bulb depression when the evaporating surface has the same temperature as the wet-bulb thermometer; it is rigorously proportional to vapor pressure deficit when the evaporating surface has the same temperature as the dry bulb. Temperatures of the evaporating surfaces of such instruments as the Piche evaporimeter and the white Livingston porous-cup atmometer, when evaporation is rapid, probably approximate the temperature of the wet bulb more closely than that of the dry-bulb thermometer.

But to return to the proportionality of rate of evaporation to difference in vapor pressure between the air immediately at the evaporating surface and in the air above. The simplest expression of such proportionality is $V = A(E_0 - e_1)$, V denoting mass of water lost (or gained) by unit area in unit time, and A a factor of proportionality. The equation would be complete if no factors other than humidity difference were of consequence. It is to be noted that this simple equation for V has the familiar form of many equations that express rate of transfer of matter or energy through space—conduction of heat, diffusion of solutes, etc.—along a gradient. But the difference $(E_0 - e_1)$ does not define a gradient; to do so it must be divided by a term defining the distance between the points where vapor pressures are E_0 and e_1 respectively. If this distance be designated δ , and the change in vapor pressure along it is linear, the gradient is defined by $(E_0 - e_1)/\delta$. The vapor pressure difference alone can therefore be used as the basis of an evaporation formula only if δ is constant for all evaporating surfaces. Since δ cannot be constant, it must be included in any evaporation formula that uses the difference $(E_0 - e_1)$. Even then, the expression $(E_0 - e_1)/\delta$ is an accurate expression of the gradient only if change in vapor pressure normal to the evaporating surface is linear. In general, and for unlimited distances from the evaporating surface, the change in vapor pressure in the direction of transfer of water vapor is not linear, the gradient is not constant. The general expression of the gradient is therefore the derivative de/dn , the change in vapor pressure along the element dn of distance normal to surfaces of equal vapor pressure. Since under a steady rate of evaporation we must assume a flow of water vapor from the evaporating surface outward to an indefinite distance, V is also the mass of water vapor passing in unit time through unit area lying in a surface of equal vapor pressure in the air at an indefinite distance from the evaporating

surface. The general expression for evaporation may therefore be written $V = A(de/dn)$, if A be taken to denote any coefficient of transfer applicable to any gradient of vapor pressure along which water vapor is transferred in passing from the evaporating surface. The equation $V = A(E_0 - e_1)/\delta$ is a special case of the more general equation, applicable where the vapor pressure gradient through a distance δ is linear.

THE BOUNDARY LAYER

The two expressions $A(E_0 - e_1)/\delta$ and $A(de/dn)$ apply, in fact, to different parts of the mass of air into which water vapor passes from an evaporating surface. We shall be concerned here only with evaporation into moving air. When air moves over a solid or liquid surface, the resistance offered by the surface to its motion produces two noteworthy effects: first, a slowing down of movement in the vicinity of the bounding

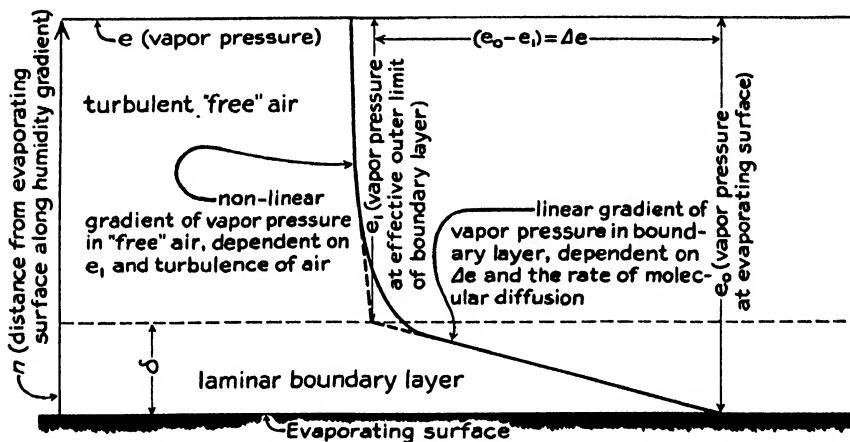


FIG. 1. Characteristic distribution of humidity in the laminar boundary layer next to an evaporating surface and in the adjacent parts of the turbulent "free" air is shown by the heavy line. The thickness of the boundary layer indicated is a mean effective thickness.

surface, so that velocity decreases to zero at the surface itself; and second, an irregular mixing—turbulence—in the air out to some indefinite distance from the bounding surface. But turbulence in the air requires freedom of movement of bodies of air of finite dimensions between layers of different mean velocity—that is, normal to the extent of the bounding surface—which freedom is gradually restricted as the bounding surface is approached. Finally turbulent motion normal to the bounding surface is completely suppressed, and in the immediate vicinity of the surface air moves in layers parallel to it between which there is no turbulent interchange: the movement of the air is laminar (fig. 1).

Now conditions for the transfer of matter or energy within the boundary layer are totally different from those which obtain in the atmosphere in

general, which is turbulent. Where air is turbulent, its properties are transported rapidly between layers having different mean velocities, with the masses of air in turbulent interchange to which the properties pertain; and except under special conditions steep gradients of velocity, temperature, or admixtures cannot exist. But in the laminar boundary layer, where no mixing by movement normal to the bounding surface takes place, heat may be transferred only by molecular conduction, momentum only by molecular friction, and gaseous admixtures, such as water vapor, only by molecular diffusion. Gradients are therefore characteristically steeper in the boundary layer than in turbulent air. Rates of molecular transfer—coefficients of heat conduction, molecular friction, and diffusion—are nearly constant within the limited thickness of the boundary layer, and this constancy of rate of transfer produces sensibly linear gradients of temperature, velocity, and humidity from the bounding surface out to the limit of the boundary layer. Outside the boundary layer, in the region of turbulent mixing, molecular transfer is negligible in comparison with molar transfer through turbulence. The intensity of turbulent mixing varies greatly with distance from the bounding surface. Hence gradients are variable in the turbulent parts of the air, normally decreasing with increasing distance from a bounding surface, as the intensity of turbulent interchange increases.

The expression for rate of transfer of water vapor through air $A(E_0 - e_1)/\delta$ is therefore applicable particularly to transfer through the boundary layer, where the gradient of vapor pressure is linear; while the expression $A(de/dn)$ is applicable particularly to the turbulent region at some distance from the evaporating surface. In the boundary layer A is the coefficient of molecular diffusion of water vapor into air; in the turbulent region A is the coefficient of intensity of turbulent mixing, or the Austausch coefficient (Wilhelm Schmidt, '25). Rate of evaporation could be defined by means of either expression if humidity gradient either in the laminar boundary layer or at a point in the turbulent region outside it were measured, and multiplied by the appropriate coefficient of transfer. The humidity gradient is easier to measure in the turbulent region than in the boundary layer, though a considerable fluctuation in humidity is always to be observed in turbulent air, and though the gradient is ordinarily much smaller than in the boundary layer. Determination of the intensity of turbulent mixing is, however, difficult. In practise, therefore, a rational theory of evaporation must proceed from consideration of the flow of water vapor through the boundary layer, where the humidity gradient is linear, and where a difference in molecular concentration of water vapor or in vapor pressure divided by a finite length expresses the gradient. The difficulty here is in determining the thickness of the boundary layer and the humidity at the evaporating surface. If the evaporating surface is a free water surface or the surface of a porous body which evaporates like a free water surface, it is enough to assume that the air at the surface has the temperature of the

surface and is saturated. If the surface is such that the air in immediate contact with it is not saturated, as in the case of a permeable or semi-permeable membrane or the surface of a solution, the humidity of the air at the surface cannot be measured directly. A method of determining it indirectly will be outlined below.

The coefficient of diffusion in non-turbulent air gives little trouble. It is a definite quantity, dependent only on temperature and pressure. But, diffusion being a molecular process, the gradient to which the coefficient of diffusion refers is a gradient of molecular concentration, not of vapor pressure.¹ The meteorologic measure of molecular concentration is absolute humidity, the expression of mass of water vapor per unit volume. In c.g.s. units it is measured as g. per cm.³; in meteorologic practise as g. per m.³ At a given temperature, absolute humidity is proportional to vapor pressure, but the proportionality is not the same for all temperatures. Vapor pressure is more easily obtained from humidity measurements than is absolute humidity. It is therefore convenient to be able to use vapor pressure gradient instead of absolute humidity gradient. The coefficient of diffusion of water vapor into air—denoted by k —also varies with temperature, and with pressure as well, so that it is possible to express rate of diffusion in terms of vapor pressure gradient as a function of temperature and pressure.

The diffusion coefficient k has, moreover, dimensions that are not readily applicable to evaporation. Expressed rigorously in c.g.s. units, it gives the mass of water vapor in grams that diffuses across an area of 1 cm.² in one second when there is a fall in concentration of water vapor of 1 g. per cm.³ in a distance of 1 cm. normal to surfaces of equal concentration. So steep a gradient is scarcely to be found in nature; and evaporation measured in grams per second from 1 cm.² of surface gives very small quantities. In the light of these considerations, I have recomputed from k a more practicable diffusion coefficient k' , which gives the amount of water vapor in mg. per hour that diffuses across a surface of 1 cm.² along a vapor pressure gradient of 1 mm. of mercury per cm. of distance measured normal to surfaces of equal vapor pressure.² The dimensions of this coefficient are in accordance with the magnitudes commonly encountered in experimental work on evaporation. The variation of k' with temperature and pressure, through a range of temperature from 0° to 50° C. and a range of pressure from 600 to 790 mm. of mercury, is shown in figure 2. Numerical values

¹ If a formula for transfer of water vapor in the turbulent part of the atmosphere were to be set up, the appropriate expression of moisture content of the air would be specific humidity: mass of water vapor per unit mass of air.

² The equations used in computing k and k' are as follows:

$$k = 0.230 \left(\frac{273 + t}{273} \right)^2 \cdot \frac{760}{p}; \quad k' = 3.6k \frac{1 + \alpha t}{1.06},$$

t being temperature in ° C., p atmospheric pressure in mm. Hg, and α the coefficient of expansion of air.

of k' may be read from this figure to the second decimal place. The temperature used in taking out a value of k' should be the mean of the temperatures of the evaporating surface and of the air in its vicinity. Figure 2 is included here more for the sake of investigations of evaporation into still air than for the purposes of the present discussion, which is concerned with moving air.

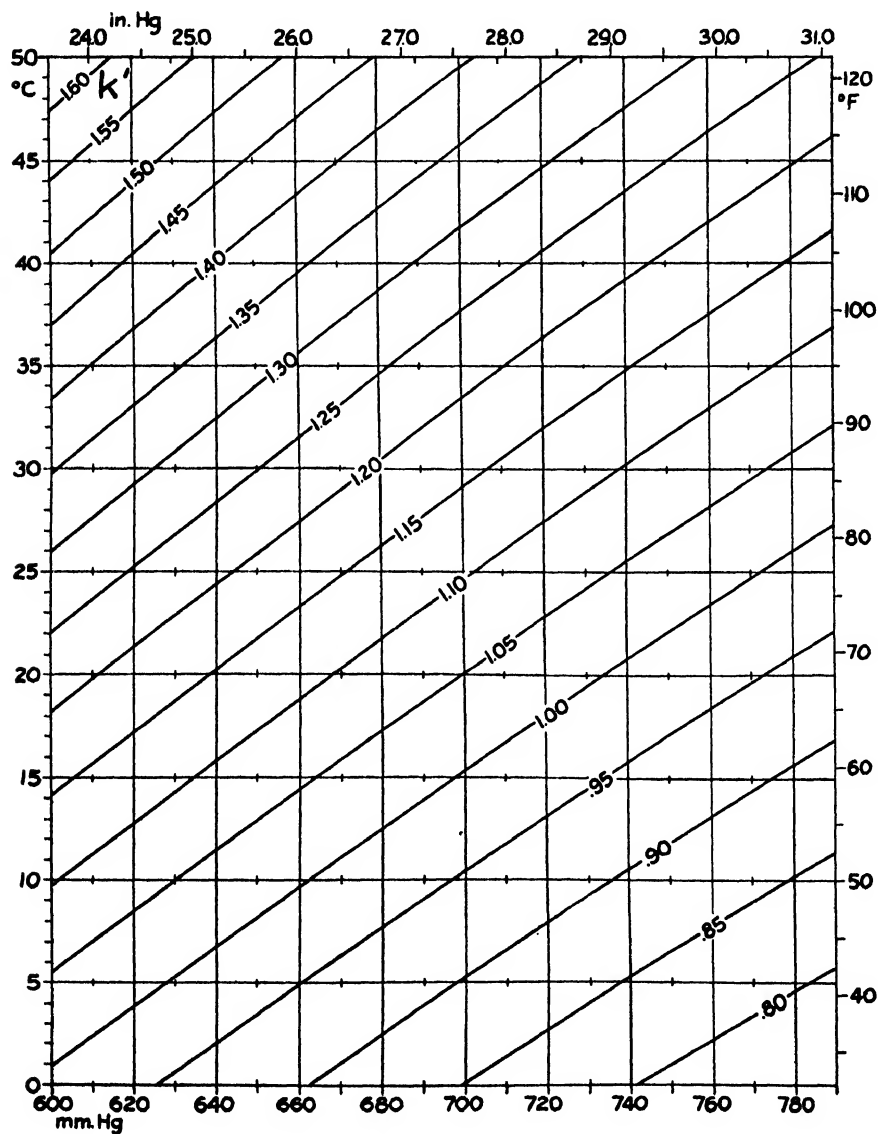


FIG. 2. Coefficient of diffusion of water vapor into air, k' , in mg./cm.² hr. for a vapor pressure gradient of 1 mm. Hg per cm. along a humidity gradient, plotted as a function of temperature and atmospheric pressure.

We are able, then, to give a physically definable value to the coefficient of transfer in the above formulation, and to express rate of evaporation as

$$V = k' \Delta e / \delta, \quad (1)$$

Δe being used for $(e_0 - e_1)$, the difference in vapor pressure between the air at the evaporating surface and at the outer limit of the boundary layer, and δ for the thickness of the boundary layer in cm. V in the equation, as a result of recomputation of the diffusion coefficient, is expressed in mg. per cm.² per hr.; δ remains to be determined.

Thickness of the boundary layer in air has been measured directly at various times and by various methods. Its order of magnitude is from a few millimeters down to some small fraction of a millimeter. Within it, gradients of vapor concentration, temperature, and velocity are linear. Fine measurements of humidity, temperature, or velocity may therefore be used to determine its thickness, as the distance outward from the bounding surface within which these qualities have a linear distribution. The thickness of the layer is the same for all the qualities enumerated, since it depends solely on the character of the flow of air in the vicinity of the bounding surface.³

The character of the flow of air past a solid or liquid surface is in turn dependent upon the relative influence (1) of movement in the air at a distance from the bounding surface and (2) of the surface itself. Movement of the "free" air (using the word "free" to designate air outside the boundary layer) tends to induce turbulent mixing in all the air continuous with it and within which there is a velocity gradient, down to the bounding surface. The presence of the surface inhibits turbulence in its immediate vicinity, but can directly only prevent movement through the surface itself. The effect of the bounding surface is extended outward by the molecular viscosity of the air. The thickness of the boundary layer at any moment represents a state of equilibrium between the "inertia" effect of the moving free air and the "frictional" effect of the fixed boundary surface. The greater the velocity of the free air, the greater the inertia effect, and the closer to the boundary surface turbulence, characteristic of the free air, extends; hence the thinner the boundary layer. The less the velocity of the free air, the less the inertia effect, the farther from the boundary surface does the (molecular) frictional influence of the surface extend, and the thicker is the boundary layer. Figure 3 shows three possible thicknesses. The least thickness, indicated by δ_1 , corresponds to the highest of three velocities in the free air, and to a maximum of the inertia effect. Thicknesses δ_2 and δ_3 correspond to smaller velocities in the free air and to rela-

³ Some results of direct instrumental measurement of thickness of the boundary layer are to be found in K. Büttner ('34). Objections have been raised against instrumental measurements on the ground that the introduction even of fine instruments into the layer disturbs it. Instructive determinations of its thickness by optical measurements which avoid any disturbance of the layer are described by Kennard ('32) and by Schmidt ('32).

tively greater frictional influence of the bounding surface. Because of mixing by turbulence in the free air, the vapor pressure at the outer limit of the boundary layer in every case approximates that obtaining in the free air; at a water surface the vapor pressure corresponds to saturation at the

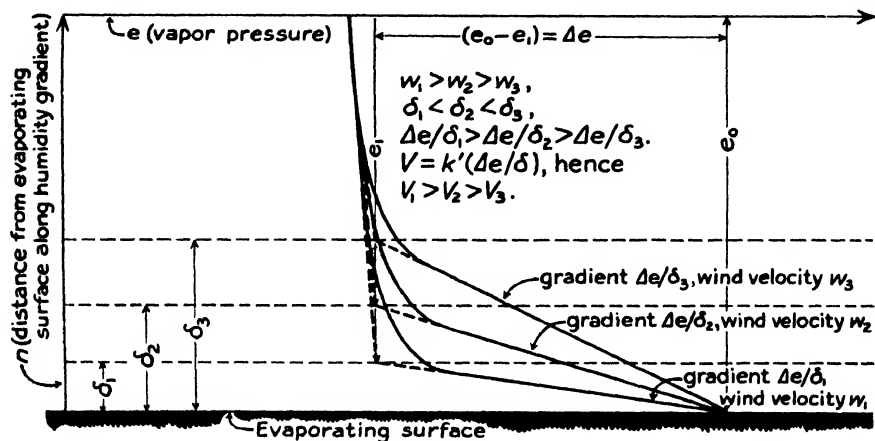


FIG. 3. Gradients of vapor pressure in laminar boundary layers of different thicknesses.

temperature of the surface. Variation in the value of the gradient $\Delta e / \delta$, vapor pressure at the evaporating surface and in the free air remaining constant, depends on variation in δ . Since the rate of evaporation is the rate of diffusion through the boundary layer, V is inversely proportional to δ .

Before the relation expressed by equation (1) is applied to experimental data, two uncertainties must be disposed of. The first is concerned with the fact that the humidity gradient in the turbulent parts of the air in the vicinity of an evaporating surface is not zero, since the occurrence of evaporation implies that there is a flow of water vapor into the air, and this flow in turn implies a gradient. If one examines experimental data, however, one finds that measurements of humidity made at a distance of a few centimeters from the evaporating surface, by ordinary meteorologic methods, give entirely acceptable results. No concern need be had except in very quiet air, in which there may be danger, if fine instruments are used, of measuring humidity within the boundary layer. Measurements made at different distances from the evaporating surface will settle any doubts that may arise, since the steep humidity gradient ordinarily encountered in the boundary layer is easily distinguished from the smaller gradient in the turbulent free air. With even a light wind, moreover, only the finest instruments can be brought close enough to the evaporating surface to be within the layer. The other uncertainty arises from variation within short periods of time in the thickness of the boundary layer. All wind is more or less gusty, and each gust may be expected to decrease its thickness, each

lull to permit it to become thicker. Evaporation measurements are not, however, instantaneous measurements, but extend over a finite length of time. In the theory developed here, it is not anticipated that thickness of the boundary layer will be measured directly, but that it will be expressed as a function of wind velocity in the free air. The integration of wind movement over the period of measurement of evaporation, performed by most anemometers, brings about an appropriate averaging. Direct measurements of the distribution of temperature in the layer do not reveal a sharp outer boundary, but a transition such as is indicated in figures 1 and 3. One is ordinarily dealing with an effective mean thickness rather than with a sharply defined quantity.

It is obvious that equation (1) applies to evaporation from surfaces at which the air is not saturated as well as from surfaces of pure water. If e_0 , vapor pressure at the evaporating surface, is less than saturation vapor pressure, as at the surface of a salt solution or on the average over the surface of a transpiring leaf, the difference Δe , and with it the rate of evaporation V , are decreased accordingly.

AN EQUATION FOR RATE OF EVAPORATION INTO MOVING AIR

Measurement of the thickness of boundary layers over evaporating surfaces offers an attractive field for future investigation, in which optical methods would appear to promise better results than direct measurements of gradients of temperature, humidity, or velocity. If the thickness is measured directly, equation (1) can be solved immediately, k' being taken from figure 2. In the meantime, the relation between wind velocity in the free air and thickness of the layer permits an indirect approach. The reader will already have noted that it is as a measure of the thickness of the boundary layer that wind velocity enters a theoretical formulation of rate of evaporation: either explicitly, as in the present formulation, or implicitly and empirically, as in more familiar equations. The factors which determine the thickness are as follows: (1) velocity of the wind in the free air, w , which operates in the manner described above; (2) length of the evaporating surface in the direction of the wind, l , thickness of the layer increasing with distance from the edge presented to the wind; (3) density of the air, ρ , which helps to determine the extent to which the momentum of the moving free air can displace the air near a bounding surface; and (4) molecular viscosity of the air, μ , which determines how far from the bounding surface air can be maintained in a laminar state through molecular friction against the tendency toward turbulent mixing exerted by the free air. The thickness of the boundary layer will clearly increase with l and μ (which measure the effect of the bounding surface in maintaining the layer) and decrease with w and ρ (which measure the effect of the free air in crowding turbulent conditions down toward the bounding surface). The thickness of the boundary layer is, then, directly

proportional to some function of $(l\mu)$ and inversely proportional to some function of $(w\rho)$. If it be assumed that the functions of the two groups of terms are identical,⁴ the entire relation may be expressed as

$$\delta \sim f(l\mu/w\rho),$$

the symbol \sim signifying proportionality, and the nature of the function denoted by f remaining to be determined.

The expression $(l\mu/w\rho)$ may be separated into two terms (l/w) and (μ/ρ) , the former of which refers to the time required for a given part of the free air to pass the evaporating surface, and the latter to the qualities of the air that are dependent upon temperature and pressure. The expression for the proportionality of δ may therefore also be written

$$\delta \sim f(l/w, \mu/\rho).$$

The second of the terms does not weigh heavily in the evaporation equation; it will appear in some power less than 1, in the case of small, smooth plane surfaces as $\sqrt{\mu/\rho}$. The term l/w , on the other hand, is a very important one, since it takes account of both wind velocity and size of the evaporating surface. We may leave the function of l/w to be determined empirically and dispose of μ/ρ by writing

$$\delta \sim \sqrt{\frac{\mu}{\rho}} f\left(\frac{l}{w}\right);$$

and return to equation (1) with this expression for δ . Equation (1) then becomes

$$V = c \frac{k' \Delta e}{\sqrt{\frac{\mu}{\rho}} f\left(\frac{l}{w}\right)}, \quad (2)$$

or

$$V = k' \Delta e c \sqrt{\frac{\rho}{\mu}} f\left(\frac{w}{l}\right), \quad (3)$$

c being a coefficient of proportionality that takes care of the relation between δ and both of the terms $\sqrt{\rho/\mu}$ and $f(w/l)$.

Since viscosity and density vary with temperature and pressure, and with them the value of $\sqrt{\rho/\mu}$, and since k' also varies with temperature and pressure, it is possible to combine k' and $\sqrt{\rho/\mu}$, despite their different logical places in the equation, into a single coefficient $k' \sqrt{\rho/\mu}$, which will be called k'' . Numerical values of k'' —which should be used only in an equation for evaporation into moving air, since the function of density and viscosity included in it relates only to the thickness of the boundary layer—may be read to the second decimal place from figure 4.⁵

⁴ The remainder of the argument hangs on this assumption.

⁵ Density computed with the aid of table 105 of *Smithsonian Meteorological Tables* (5th ed., 1931), and μ according to the formula

$$\mu = .0001824 - .000000493(23.0 - t),$$

where t is temperature in ° C.

The evaporation equation then becomes finally

$$V = k'' \Delta e c \cdot f(w/l), \quad (4)$$

and the unknown function of w/l may be found empirically. All experimental data indicate that it has the form $(w/l)^n$, where n is an exponent expressing rate of change in thickness of the boundary layer with change

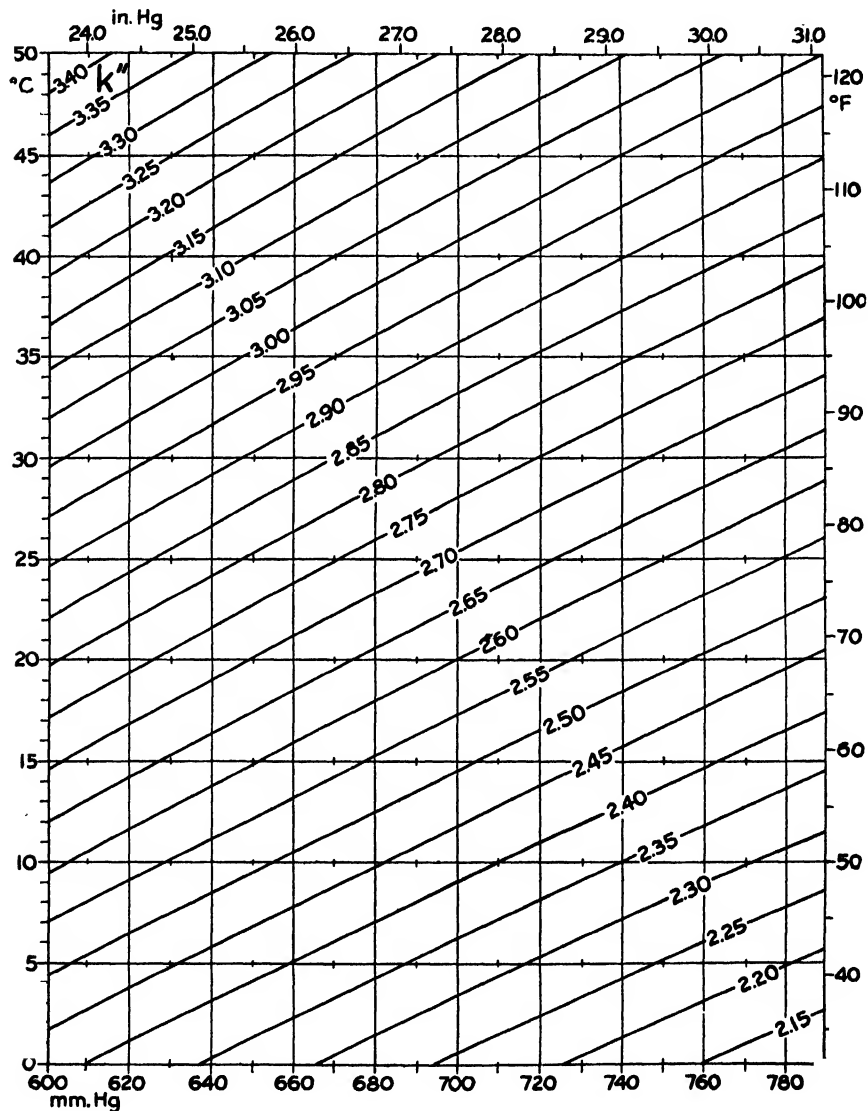


FIG. 4. Coefficient k'' , which includes all direct effects of temperature and pressure in diffusion through a boundary layer, plotted as a function of temperature and atmospheric pressure.

in w or l or both. The terms c and n may be expected to differ with surfaces of different form.

Published experimental data available to me do not permit an adequate discussion of variations in c and n in evaporation from different forms of surface. In the case of regular plane surfaces of sizes used in experimentation n is about 0.5, so that $(w/l)^n$ is about $\sqrt{w/l}$. This value is in accordance with the conclusions of many experimenters, that with plane surfaces of constant form and size rate of evaporation varies as the square root of wind velocity. For evaporation from a small wet-bulb thermometer (data from Seybold, '29, pp. 61-62) I find a value for n of 0.3. Experimenters at the British National Physical Laboratory found that evaporation from a cylindrical surface placed transversely to a wind stream varied as the 0.7th power of wind velocity.⁶ Systematic investigation of the function of w/l for different kinds of surfaces must await the time when evaporation observations are reduced according to a rational equation or when experimenters make available all the data pertinent to their experiments.

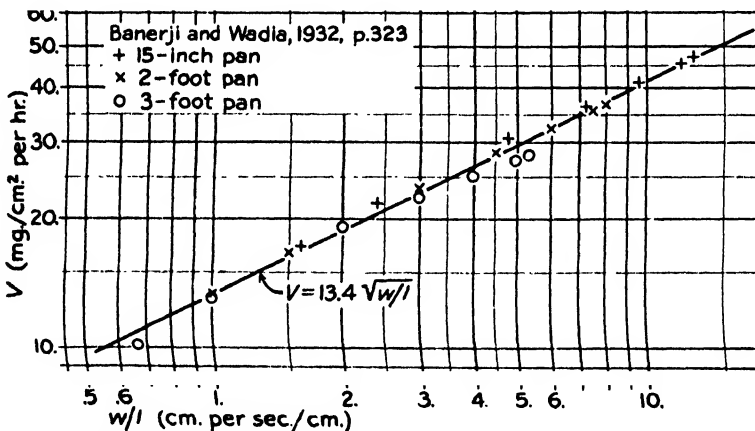


FIG. 5. Relation of rate of evaporation from square experimental pans to wind velocity and size of evaporating surface.

Only one demonstration will be given here of the relation between rate of evaporation and w/l : the material plotted in figure 5. The data (Banerji and Wadia, '32, p. 323) are from a good set of measurements of evaporation from pans 15 in., 2 ft., and 3 ft. square, the wind blowing parallel to one side of the pans. In figure 5 rate of evaporation, in $\text{mg./cm.}^2 \text{ hr.}$, is plotted on the scale of ordinates and w/l on the scale of abscissas. Both scales are logarithmic. The straight line in the figure is the graph of the equation $V = 13.4 \sqrt{w/l}$; it fits the plotted points very well. The authors cited did not publish temperature, pressure, and humidity observations with the data, and so a complete solution of equation (4) cannot be given.

⁶ Reported in *Engineering* 138: 362, 1934.

Use of the formulation $(w/l)^n$ as the empirical function of w and l must be justified by the results of experiment, and in order to be judged critically must be applied to a large amount of experimental data. Application of the equation by those who may have or acquire fuller experimental material than I have had at my disposal is easy. It is only necessary to plot $V/k''\Delta e$ against w/l on logarithmic coordinate paper, from the slope of the line that all good data yield determine the exponent n , and from the intersection of the line with the abscissa 1.0 the coefficient c . Data from surfaces of different form should be handled separately. Figure 5 aims only to demonstrate that size of evaporating surface, as it affects rate of evaporation per unit area, is taken care of by combining it with wind velocity in the expression w/l .

From working with a large amount of published material, I find the procedure satisfactory for surfaces ranging in size from Seybold's small thermometer bulb (surface area 1 cm.²) up to evaporation pans 4 ft. in diameter. The values of c and n derived from measurements with experimental evaporation pans did not give good results with the data from a circular reservoir 85 ft. in diameter (Rohwer, '31). There must be an upper limit to the dimensions of evaporating surfaces for which it is valid; namely, at the dimension beyond which increased length of the surface in the direction of wind movement ceases to affect the mean thickness of the boundary layer. Over extensive surfaces the boundary layer must attain a limit of thickness, beyond which it remains constant at a given wind velocity, while w/l decreases indefinitely with indefinite increase in the value of l . This limitation might possibly be taken care of by making n such a function of l that it approaches 0 as l becomes large, but as yet this possibility cannot be investigated. To judge from the material I have worked with, the limit seems to be attained somewhere between $l = 4$ ft. and $l = 85$ ft. At present I cannot say whether or not there is a lower limit to its validity.

RELATION OF THE THEORY TO TRANSPIRATION PROBLEMS

Equation (4) is of general applicability to surfaces within the range of size with which most biologic investigations are concerned. The only significant factor omitted from it is roughness of the evaporating surface, and that factor is, to a certain degree, taken care of by the empirical terms. The effect of roughness is ordinarily to make the boundary layer thicker than it would be over a smooth surface of the same form and dimensions, but the qualitative differences in roughness are so great that it does not seem worth while to attempt to include in the equation a quantitative formulation of its effect. The extreme effect of roughness, among leaf surfaces, may be seen in the case of a coating of (non-transpiring) hairs so closely spaced that the surface defined by their outer ends acts as a boundary surface against which the non-turbulent boundary layer of air is formed,

instead of next to the actual transpiring surface, as in the case of a smooth leaf. The thickness of the boundary layer is thereby increased by the length of the hairs, and the gradient of vapor pressure decreased accordingly. The effective cross-sectional area above a square centimeter of leaf surface through which water vapor may diffuse is decreased by the sum of the cross-sectional areas of the hairs on the unit area of leaf surface. Where the hairs are matted, the effective free space through which vapor may diffuse from unit area of the leaf is further reduced. These considerations indicate the possibility of evaluating a hairy leaf-coating in terms of the resistance it offers to transpiration.

The theory permits a rational approach to the much-debated question of "transpiration resistance" (cf. Seybold, '33, and literature cited there). One type of transpiration resistance was mentioned in the foregoing paragraph, the effect of which is to decrease rate of evaporation by thickening the boundary layer of non-turbulent air. Other "resistances" weaken the vapor-pressure gradient in the boundary layer by decreasing the vapor pressure at the transpiring surface, first below that which obtains at a free liquid surface (an effect exerted by the interposition of any membrane), and then below that which obtains at the outer surface of a thin epidermis. Thickening of epidermis and waxy coverings belong here. As for the effect of number of stomata per unit leaf area and degree of closing of these, it would appear that they may be handled quantitatively by using a mean vapor pressure at the surface of the leaf. The surface vapor pressure can be known directly only over a free liquid surface, of pure water or of a salt solution of known concentration. The vapor pressure at leaf surfaces can probably be found only indirectly, through comparison of measured transpiration rates with measured rates of evaporation from evaporimetric surfaces which behave as free water surfaces and have the same form and most conveniently the same dimensions as the leaves. Identity of dimension is not, however, obligatory, since the term in which linear dimension appears in equation (4) is w/l ; if the dimension l of the evaporimetric surface is larger or smaller than the same dimension of the leaf surface under investigation, w/l may be kept constant by increasing or decreasing the velocity of the wind w in the same ratio.

Assume that an ideal evaporimetric surface and the leaf surface have the same temperature. If the rate of evaporation from the evaporimetric surface be designated V_0 , rate of transpiration (in the same units) from the leaf surface V_p , vapor pressure at the evaporimetric surface E_0 , at the leaf surface e_p , and in the free air e_1 , then with the same value of w/l

$$V_p : V_0 = (e_p - e_1) : (E_0 - e_1);$$

or if for brevity's sake we set Δe_p for $(e_p - e_1)$, Δe_0 for $(E_0 - e_1)$,

$$V_p : V_0 = \Delta e_p : \Delta e_0.$$

Now $V_p : V_0$, or its equivalent $\Delta e_p : \Delta e_0$, is a rigorous expression for the

relation aimed at by the familiar ratio "relative transpiration." "Relative transpiration," as ordinarily used, is no such definite quantity, since the rates of loss of water compared by it refer to surfaces which may have very different physical qualities. *Dependence of thickness of the boundary layer on form and size of surface forbids the indiscriminate comparison of rate of transpiration from leaf surfaces of different sizes and shapes with evaporation from any arbitrarily selected type of evaporimetric surface, be it plane, cylindrical, or spherical.* If a rigorous comparison is to be made, it must be between surfaces which behave similarly, from an aerodynamic viewpoint, in wind; that is, which have the same form and for which w/l is constant. It was recognition of this principle, though expressed in different terms, that led Seybold ('29, pp. 19 ff.; '32) to reject "relative transpiration" and to advocate the use of evaporimetric surfaces of the same shape and size as the transpiring surfaces under investigation.

The ratio $V_0 : V_p$, or $\Delta e_0 : \Delta e_p$, is Seybold's "transpiration resistance," obtained by dividing rate of transpiration into rate of evaporation from a free water surface of the same size and shape and having the same temperature; that is, having the qualities of our ideal evaporimetric surface. Seybold has vehemently denied that his "transpiration resistance" is merely the reciprocal of "relative transpiration"; and rightly, if relative transpiration is computed from measurements made with the aid of evaporimetric surfaces of arbitrary form. But if an evaporimetric surface is aerodynamically similar to a transpiring leaf surface and has the same temperature, the rigorous expression of "relative transpiration" $V_p : V_0$ or $\Delta e_p : \Delta e_0$ is the reciprocal of "transpiration resistance."

It is not my business to tell the ecologist or plant physiologist which of the two essentially equivalent expressions he should use. But if the phenomenon under discussion be considered merely one of a large class of physical processes involving transfer of matter or energy, it is more in accordance with general physical practise to use the ratio $V_p : V_0$ or its equivalent ratio of vapor pressure differences than $V_0 : V_p$, or its equivalent. It is a sort of "transmission coefficient" of water vapor from unit area of leaf surface, having a maximum value of 1.0 when transpiration is equal to evaporation from an aerodynamically similar free water surface having the same temperature.

Determination of the rigorous "relative transpiration" ratio $V_p : V_0$ or of the "transpiration resistance" ratio $V_0 : V_p$ would proceed approximately as follows:

A model of the transpiring surface (if a leaf, preferably made of paper or cardboard that will imbibe a considerable quantity of water, since such a model evaporates most of its imbibed water at the same rate as a free water surface) is constructed and exposed to wind in the same manner as the leaf or aggregation of leaves to be investigated. When the temperature of the surface has become constant, indicating the attainment of a constant

rate of evaporation, the temperature is recorded, together with wind velocity, pressure, temperature, and vapor pressure of the air into which evaporation is taking place. Repeated weighings permit the computation, in appropriate units, of rate of evaporation. Measurements should be made at two or preferably more wind velocities.

The temperature of the surface of the model will not be the same as that of the leaf. Rate of evaporation from the model is not, therefore, V_0 in the ratios. To keep the terms pertaining to the model distinct from those pertaining to the leaf and the ideal evaporimetric surface, rate of evaporation from the model will be denoted by V_0' , vapor pressure at its surface by E_0' , and the difference in vapor pressure between its surface and the free air by $\Delta e_0'$. The vapor pressure difference to be introduced into equation (4) is then the difference $\Delta e_0'$ between maximum vapor pressure at the temperature of the surface of the model and the vapor pressure obtaining in the air. The term k'' may be taken from figure 4, using for temperature the mean of the temperatures of the evaporating surface and of the air. $V_0'/k''\Delta e_0'$ is then computed and plotted against w/l on logarithmic coordinate paper for the several values of w used in the experiment, and c and n determined for the surface. The leaf or aggregation of leaves to be investigated is then placed under the same conditions and its rate of transpiration, V_p , expressed in the same units as V_0' , measured, together with its surface temperature. The terms c and n being known for the leaf from the measurements of evaporation from the model, they may be substituted, together with the value of k'' appropriate to the temperature of the leaf, in the equation

$$V_p = k''\Delta e_p c(w/l)^n, \quad (5)$$

and the equation solved for Δe_p , the difference in vapor pressure between the leaf surface and the air. The vapor pressure e_1 of the air being known, e_p is $e_1 + \Delta e_p$. Humidity tables give immediately the saturation vapor pressure at the temperature of the leaf surface, which is E_0 of our ideal evaporimetric surface, so that Δe_0 may be easily computed as $(E_0 - e_1)$. Either ratio $\Delta e_p : \Delta e_0 = V_p : V_0$ (rigorous "relative transpiration") or $\Delta e_0 : \Delta e_p = V_0 : V_p$ (transpiration resistance) may then be computed.

All the measurements prescribed in the foregoing have been made repeatedly in the course of transpiration investigations (e.g., Seybold, '29). It is not necessary to measure transpiration from the leaf under the same temperature and wind conditions as evaporation from the model. It is not necessary to perform the measurements in the dark, since the effect of radiation is taken care of by measurement of the temperatures of the evaporating and transpiring surfaces. The only empirical term is the function of wind and size of surface $c(w/l)^n$, common to model, leaf, and ideal evaporimetric surface. Leaves of the same shape as the model must be used, and exposed in the same position relative to the direction of the wind; but they may be of different sizes, wind velocity being adjusted

accordingly, since w/l takes care of difference in size. The gain made by using the equation is that the number of empirical terms to be dealt with is reduced to very nearly a minimum, so that the other variables may be given their theoretical values.

A word may be said in conclusion concerning the wind conditions under which transpiring leaves find themselves in nature. Most of them are exposed to the free movement of turbulent air. So long as the air in the vicinity of the leaves is turbulent, each leaf will have its boundary layer surrounding it like a sheath, and equation (5) will apply to the loss of water vapor from its surface. The boundary layers about several neighboring leaves become thicker with decreasing wind velocity, and eventually may coalesce. If branches and leaves are crowded, the boundary layer may then become continuous about a considerable number of leaves. The thicker the boundary layer, that is, the greater the distance from a leaf surface to turbulent air, the less the vapor pressure gradient in the boundary layer, and the slower the transport of water vapor through it. Weakening of turbulence and consequent thickening of the boundary layer probably reach a maximum in the interior of dense cushion plants and among the grass of closed sods. Absence of wind movement sufficient to register on ordinary meteorologic anemometers must not be taken as evidence that wind velocity is to be set equal to zero. More sensitive instruments (cf. the one described by Stålfelt, '32, pp. 50-51) may reveal measurable movement of the air.

Equations (4) and (5) give zero evaporation at zero wind velocity. Though this result may appear erroneous, it is none the less logical. Only in perfectly still air, and when the evaporating surface has the same temperature as the air in its vicinity, is rate of evaporation determined by pure diffusion to an indefinite distance from the evaporating surface. Under such conditions, the rate of evaporation will clearly decrease as the air surrounding the evaporating surface takes on more and more water vapor, and approach zero as the air at the farther limits of diffusion approaches saturation. It is possible to solve the problem of varying rate by taking into account the dimensions of the space into which diffusion takes place. But the conditions involved are so remote from those under which plants or experimental evaporimetric surfaces are ordinarily exposed that there is little to be gained by investigating the variable rate of evaporation they would permit. Under special laboratory conditions it may be advisable at times to use the assumption of pure diffusion beyond the immediate vicinity of an evaporating or transpiring surface, and to apply the coefficient k' plotted in figure 2. No solution of general applicability is possible.

SUMMARY

A theory of the dependence of rate of evaporation (into moving air) is elaborated: it is based on the hypothesis of the existence of a laminar

boundary layer of air, having a thickness that varies with wind velocity, next to the evaporating surface. Rate of evaporation then becomes equivalent to rate of molecular diffusion of water vapor through this layer. All the terms involved in an expression for rate of diffusion through the boundary layer can be given a rational expression except thickness of the layer. For small surfaces, such as the transpiring surfaces of plants and evaporimetric surfaces, its thickness may be expressed as an empirical function of wind velocity and length of the evaporating surface in the direction of movement of the wind. Available experimental data seem to show that this thickness is proportional to a power smaller than unity of the quotient obtained by dividing wind velocity by the linear dimension of the surface measured in the direction of wind movement.

The theory thus developed is then used as the basis of a more rigorous definition of "relative transpiration" than has heretofore been formulated. An experimental procedure is described whereby this rigorous "relative transpiration" or its reciprocal, "transpiration resistance," may be obtained. Experimentation directed toward this end must, however, make use of evaporimetric surfaces that are aerodynamically similar to the transpiring surfaces under investigation, rather than of evaporimeters having arbitrarily selected sizes and shapes.

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FOOD HABITS OF ADULT PHEASANTS IN MICHIGAN BASED ON CROP ANALYSIS METHOD

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This investigation of the food habits of the pheasant ¹ was centered in the general farming region of southern Michigan. Data were collected from June 1930 to July 1, 1933.

The food habits of the ring-necked pheasant have been investigated to some extent by other workers in several parts of the United States. McAtee ('12) reported on a few stomachs collected during the fall months in Washington and Oregon. Burnett ('21) reported on the crop analyses of 45 pheasants collected near Fort Collins, Colorado, during all seasons of the year. A count was made of all food items, but no percentages were computed. Maxson ('21) made a report on the crop and gizzard analyses of 12 male pheasants collected in summer, fall, and early winter near Longmont, Colorado. He interpreted the data in respect to the economic status of the pheasant in the particular area where the investigation was conducted. Another investigation was conducted by Cottam ('29) in Utah County, Utah. Pheasants were collected at all seasons of the year. The results were based upon the crop and gizzard analyses of 45 pheasants. The volumetric methods used in analyzing the various foods were the same as those employed by the U. S. Biological Survey.

A more extensive study of the food habits of the pheasant was undertaken by Swenk ('29) in Valley County, Nebraska. The crops and gizzards of 100 pheasants collected in every month of the year were examined. Results were based upon net weight.

Severin ('33) made a report on the stomach analyses of 285 adult pheasants collected in South Dakota during all months of the year. Results and interpretations are based upon the numerical method of stomach analysis. The investigation was conducted primarily to determine the economic status of the pheasant in that state.

Leffingwell ('28) described the general feeding habits of pheasants from birds collected from various parts of the United States, but gave no quantitative data upon the foods eaten throughout the year. The method of analysis was by counting rather than by weight. In addition to the above-mentioned

¹ The introduced pheasant in Michigan is a mixture of *Phasianus torquatus* Gmel., the Chinese ring-necked pheasant; *Phasianus colchicus* L., the Caucasian pheasant, or so-called English blackneck, and *Phasianus versicolor* Vieillot, the green Japanese pheasant. Probably very few Chinese ringnecks occur in the state.

investigations, some shorter articles and notes concerning the food habits of the pheasant in the United States are to be found scattered through ornithological literature.

Dry weight was used in this investigation as the method of analyzing crops and computing percentages. This method not only shows the kind and amount of food eaten, but also makes possible the expression of food constituents, proteins, fats, and carbohydrates in generally accepted terms. The method does, however, tend to overemphasize the grains eaten during the summer as compared to insects.

The technic of crop analysis by the dry weight method was as follows: The contents of each crop were placed in a number 40 mesh sieve and the fine sand washed out. The food was then placed on a glass tray and the various items separated, identified, and put separately into small petri dishes. They were then dried in an electric oven. All items were allowed to remain in the oven until they had ceased to lose weight. Only ten to fifteen dishes were removed from the drying oven at one time so that the materials were exposed to the air for the minimum period. As a further precaution against possible absorption of moisture from the air while weighing, a glass desiccator was used to hold the dried materials when they were not actually on the balance. An analytical balance sensitive to .001 of a gram was used in weighing the dried crop contents. This permitted the accurate weighing of very small items of diet.

The percentages were based upon the total quantity of each item in all of the crops for a given period of time, and not upon the individual crop as a unit. Thus the individual variations which occur in the feeding habits were partly eliminated.

FEEDING HABITS

Adult pheasants usually do not commence feeding as soon as they leave the roost, but wander about, taking little or no food until about an hour after sunrise. During this period they frequently may be observed crossing roads, in lanes, or along borders of open fields. In summer the early morning activity consists mostly of playing or exercising, while in the winter it is usually spent in standing or crouching under shrubby or herbaceous cover.

In the course of this study ² pheasants were collected at all seasons of the year, and at all hours of the day. Thus the crop analysis gives much informa-

² Agencies that have cooperated in this project at one time or another are the Izaak Walton League of America, the Michigan Dept. of Conservation, the Michigan Dept. of Agriculture, the U. S. Biological Survey, the Sporting Arms and Ammunition Manufacturers Institute, the American Game Association, the Michigan State College, the University of Michigan, the Williamston Progressive Hunting Club, and other farmers in Williamston Township, Ingham County, Michigan. Particular credit is due Mr. Harry F. Harper, without whose enthusiastic moral support and generous financial backing, the project would have been impossible. The project was directed by Professor H. M. Wight, of the School of Forestry and Conservation, University of Michigan.

tion concerning the daily feeding periods. Curve *A*, in figure 1, shows the average amount of food in the crops during the course of the day and is based upon the analysis of 352 crops. Curve *B* represents the percent of pheasants observed feeding throughout the day. This curve is based upon the observations of 3,832 pheasants during all seasons of the year. Both curves indicate that the feeding period in the morning is at the maximum between one and

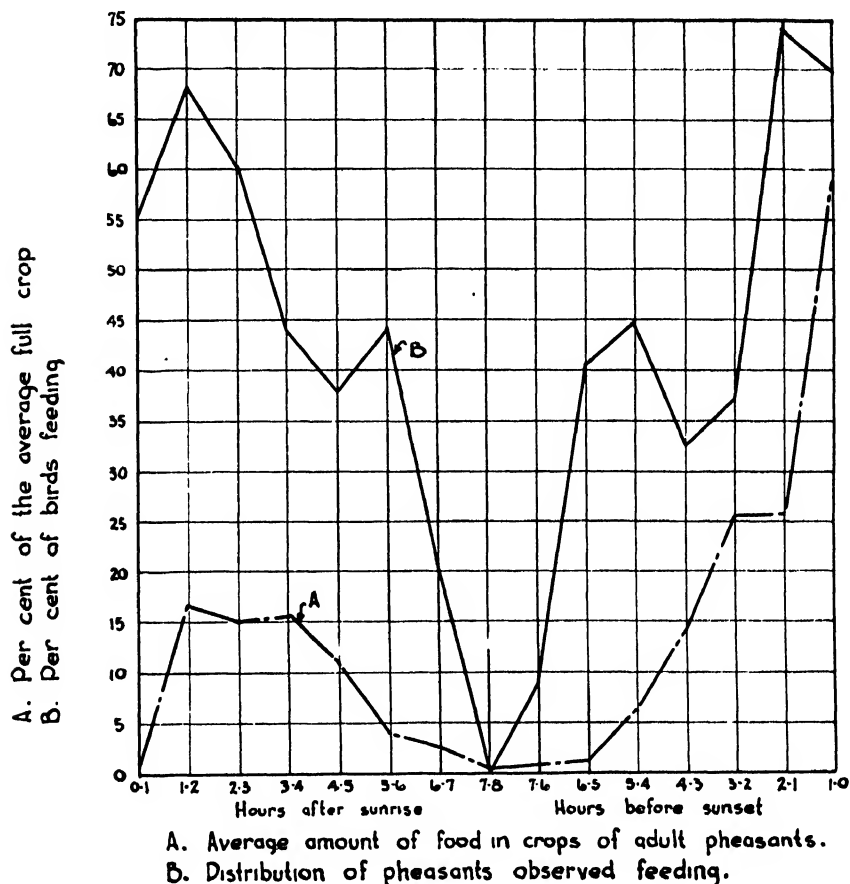


FIG. 1. Graph of pheasant feeding during the day.

two hours after sunrise.³ The rapid increase in the number of pheasants observed feeding after the first hour is due to the fact that a pheasant fills its entire digestive tract with food before there is a marked decrease in feeding activity. At noonday practically all pheasants are inactive, and with a minimum amount of food in their crops. Of all the pheasants observed during

³ The official time given by the U. S. Weather Bureau is the hour of sunrise or sunset upon which all the calculations are based.

the noonday period, 91 per cent were inactive, and none were observed feeding.

Although the number of pheasants observed feeding during the first three hours after mid-day increased rapidly, the crop analysis curve indicates that little food was eaten. The intensive afternoon feeding period begins about four hours before sunset and continues until roosting time. The maximum number of pheasants observed feeding occurred one to two hours before sunset. At this time of the day, nearly 75 per cent of the birds were feeding. By sunset the number of feeding birds had declined to 70 per cent, the remaining 30 per cent were either inactive, standing in fence rows, road lanes, fields, sitting on fences, walking, or flying toward their roosting areas.

Table I shows, in addition to the daily distribution of food per hour, the average crop weight and the number of birds collected in each period. All calculations are based upon a full crop, as found in wild birds. The average of the fifty heaviest crops was taken as 100 per cent. On this basis it was found that the average maximum crop content was 19.02 grams. All pheasants do not go on the roost with full crops. Out of 63 pheasants collected at sunset or during the hour before, only 9 had eaten more than 19 grams. Although the crop may not be full at roosting time, it was found that pheasants usually have the other parts of the digestive tract full of food by sunset. Occasionally an exceedingly heavily filled crop may be found. For instance, of 352 pheasants, one was collected with 50 grams of food in its crop. The bird was a female, killed the last week in April, and was probably an incubating bird.

TABLE I. *Average weight of crops collected at different hours throughout the day*

Hours after sunrise	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
No. of birds	10	35	21	37	31	3	4	2
Av. crop wt. in grams	.13	3.14	2.86	2.90	2.11	.78	.49	.02
Per cent av. full crop	.67	16.5	15.05	15.25	11.10	4.09	2.58	.08
Hours before sunset	8-7 ⁴	7-6	6-5	5-4	4-3	3-2	2-1	1-0
No. of birds		1	3	9	22	19	27	63
Av. crop wt. in grams			.19	1.36	2.70	4.86	4.86	11.54
Per cent av. full crop			1.00	7.15	14.20	25.53	25.53	60.66

⁴ No bird collected during this period, interpolated in chart.

In addition to seeds, fruit, and arthropods, pheasants eat much green food. Even though there may be 3 to 6 inches of snow on the ground, there are usually bare grassy spots in pastures, along ditch banks, or marsh borders where such food is available. In winter, the birds frequent such places and may be observed feeding upon grass. If no grain or seeds are easily available, they may feed exclusively on grass for short periods. The relatively high amount of grass eaten in the winter may thus be partly accounted for.

The pheasants diet is not entirely limited to food which is on or near the ground. For instance, burdock is frequently eaten in the winter and in order

to obtain the seeds, the birds must sometimes jump as high as 2 to 3 feet. Where any amount of feeding has been done on burdock, the burs become matted together. This plant, while essentially an emergency food, is sometimes eaten consistently by certain individuals when burdock is abundant. The burs are not always completely broken apart before being eaten. Burdock seeds in winter are usually heavily infested with the larvae of a moth (*Metzneria lappella* L.). In eating the seeds the birds consume the larvae as well. Pheasants also jump for the fruits of grape, nightshade, rose, and pokeberry. Occasionally pheasants are observed in apple trees, feeding on dried or frozen fruit.

Habit seems to play an important part in the feeding of pheasants. Once discovered, an area of abundant food will be visited repeatedly, often at regular intervals. In one case a flock was observed feeding upon frost grapes in an isolated area between two large grain stubble fields. Repeated observation showed the flock at this point at approximately the same hour each afternoon over a month's period during the winter. At the end of the winter the grape vines had been stripped entirely of their fruit.

On several occasions incubating hen pheasants have been observed feeding upon newly planted corn adjacent to wild herbaceous areas. The behavior exhibited by these hens resembled very closely the actions of domestic incubating hens. As soon as the hen pheasants came out into the cornfield, they fed rapidly for a half hour, occasionally pausing to stretch their wings and legs. Once a hen was seen to flap her wings during the feeding interval. In each instance, the hens appeared in the field from 4 to 4:30 p.m., approximately 3 to 4 hours before sunset and left as quickly as they had appeared. A cock pheasant was always seen with the hens. While the females fed rapidly, the cock bird appeared to be content to display and utter his grunting sound.

The pheasant is monivorous and takes almost any small animal or plant food accessible and abundant. This characteristic has enabled the bird to become established and increase in regions where natural and cultivated foods are very different from those in its native habitat in Eastern China. Cultivated grains, however, play an important part both in this country and in China (Beebe, '26).

In southern Michigan, we have records of 106 plant species being eaten by pheasants. In this list are representatives of 42 families. The grasses, Gramineae, are represented by 19 species, of which the cultivated grains form the most important part. The Rosaceae follows second with 10 species represented, and the Leguminosae with 7 species. The Compositae rank fourth with 6 species. One species, ragweed (*Ambrosia artemisiifolia*), is especially important as a food, and is available from September until April or May, an availability period lasting as long as waste field corn. One other species in this family, burdock (*Arctium minus*), is sometimes an important food in times of deep snow, and constitutes an excellent emergency food. The variety of species eaten is greatest in October, when the greatest number of plants

are bearing seeds and fruits. The minimum variety occurs in July when few wild plants are in seed and the diet consists principally of grain and insects (fig. 2).

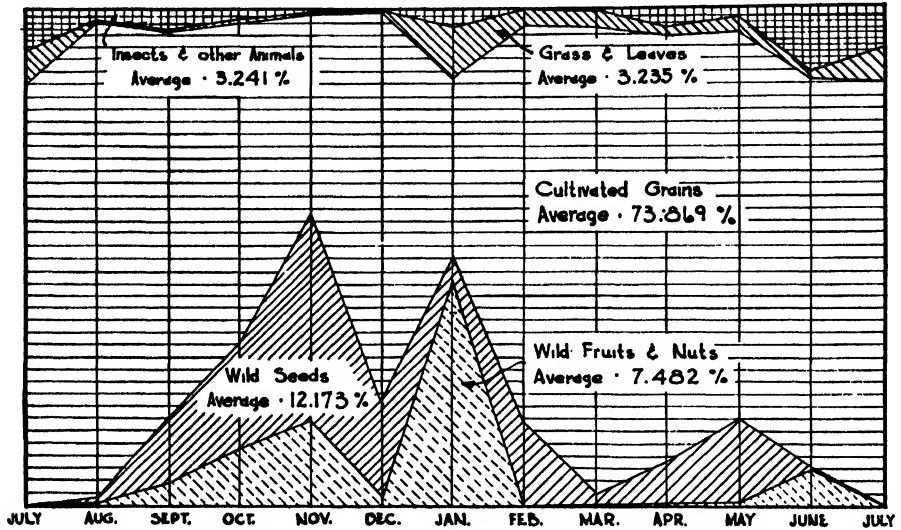


FIG. 2. Food of adult pheasants, showing the varying quantities of the principal foods and the average of each group.

In the following sections we shall present the information obtained from crop and gizzard analyses, supplemented by general observation. These data are based upon the examination of 352 crops; of this number, 86.36 per cent, or 304 pheasants, had food in their crops. Table II shows the number of pheasants examined each month.

TABLE II. *Number of pheasants collected by months (1930-1933)*

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
15	6	11	12	6	8	5	17	42	182	23	25

The vegetable constituents amount to 94 per cent of the annual food of adult pheasants. Cultivated grains form the major portion. Corn, wheat, barley, oats, buckwheat, and beans make up 74 per cent of the food for the year. Not only the adult pheasants but the young as well are highly granivorous.

The proportions of the various species of grain are shown in table IV. It would appear from these data that the pheasant is a rather expensive bird for the farmer to support, but, as we shall see, the bulk of the grains eaten are from field waste and from manure spread on the fields. Wheat and corn,

TABLE III. *Percentages of the principal foods of adult pheasants*

	Cultivated grains	Wild seeds	Fruits and nuts	Insects	Grass and leaves	Other animals
January per cent	35.957	4.480	45.751	3.581	10.231	0.000
February per cent	80.203	16.751	0.000	0.000	3.046	0.000
March per cent	86.083	2.896	0.308	0.006	10.707	0.000
April per cent	85.370	8.374	0.496	1.238	1.634	2.888
May per cent	77.532	17.043	0.594	0.640	3.307	0.884
June per cent	77.988	0.236	7.585	13.174	1.017	0.000
July per cent	84.527	0.000	0.000	8.240	7.162	0.071
August per cent	95.226	1.541	0.320	1.948	0.881	0.084
September per cent	78.525	13.182	4.243	3.891	0.107	0.052
October per cent	64.977	21.089	11.684	1.836	0.347	0.067
November per cent	40.684	41.699	17.108	0.268	0.238	0.003
December per cent	79.349	18.791	1.693	0.024	0.143	0.000

TABLE IV. *Per cent of cultivated grains eaten to the total yearly food and the percentage of each species of grain to the total amount of grain consumed*

Species	Per cent of year's food	Per cent of total grain eaten
Corn	33	45
Wheat	20	27
Barley	8	11
Beans	5	7
Oats	5	6
Buckwheat	3	4
	74	100

then, are the two most important grains in the food of the adult pheasant. The other three grains are less important, but even barley, which amounts to only 8 per cent, occurred in the crops in larger quantities than did ragweed, the most commonly eaten wild seed. These proportions will of course vary greatly in different localities depending upon the type of farming and the kinds of food available. It seems clear that if less waste grain were available, a larger proportion of weed seed would be eaten. The variation in the consumption of grain from month to month is presented in table V.

Wheat disappears from the diet in April, May, and June, but appears again with the harvesting of this grain. The large proportion of barley eaten in April and May comes from waste grain in newly sown fields. There is little need for pheasants to attempt digging out the newly sown grain for

TABLE V. *Percentage of the species of cultivated grain eaten of total food consumed for each month*

	Corn	Wheat	Barley	Beans	Oats	Buckwheat	Totals
Jan.	34	2	0	0	trace	0	36
Feb.	72	6	0	1	1	0	80
Mar.	47	40	0	0	0	0	87
Apr.	33	0	23	trace	2	27	85
May	28	trace	36	0	14	0	78
June	0	0	0	54	24	0	78
July	0	83	0	0	2	0	85
Aug.	1	73	15	0	6	0	95
Sept.	33	23	18	trace	1	3	78
Oct.	50	5	3	1	3	2	64
Nov.	28	6	2	3	2	0	41
Dec.	75	2	0	2	trace	0	79

there is usually much waste dropped at the ends of the fields. This is also true of the other small grains that are drilled. The highest percentage of grain consumed for any one month came in August, when wheat, barley, oats, and corn made up 95 per cent of the month's food. The low percentage in January is due chiefly to the presence of snow on the ground which covered the stubble fields.

In table VI is shown the distribution of the various grains during the spring, summer, autumn, and winter months.

TABLE VI. *Distribution of the total amount of cultivated grain eaten by adult pheasants for each season of the year*

Species	Summer	Fall	Winter	Spring	Totals
Corn	0.1	9.2	15.0	8.9	33.2
Wheat	0.8	3.3	13.0	2.8	19.9
Barley	1.2	1.9	0.0	4.9	8.0
Beans	4.5	0.4	0.3	0.0	5.2
Oats	2.6	0.5	0.1	1.3	4.5
Buckwheat	0.0	0.4	0.0	2.3	2.7
Totals	9.2	15.7	28.4	20.2	73.5 ± 15

In the general farming region, corn and wheat are the most important grains during the winter. Figure 3 shows that corn is eaten to a greater extent in winter than during the fall months. The chief source of all corn eaten, however, is field waste, and in the spring the source of this corn is often from manured fields. Although the data indicate that many beans are eaten in summer, this food was actually eaten only in early June. Buckwheat was eaten in the largest quantity during the spring and must therefore be waste grain.

The total amounts of plant and animal food eaten each month of the year

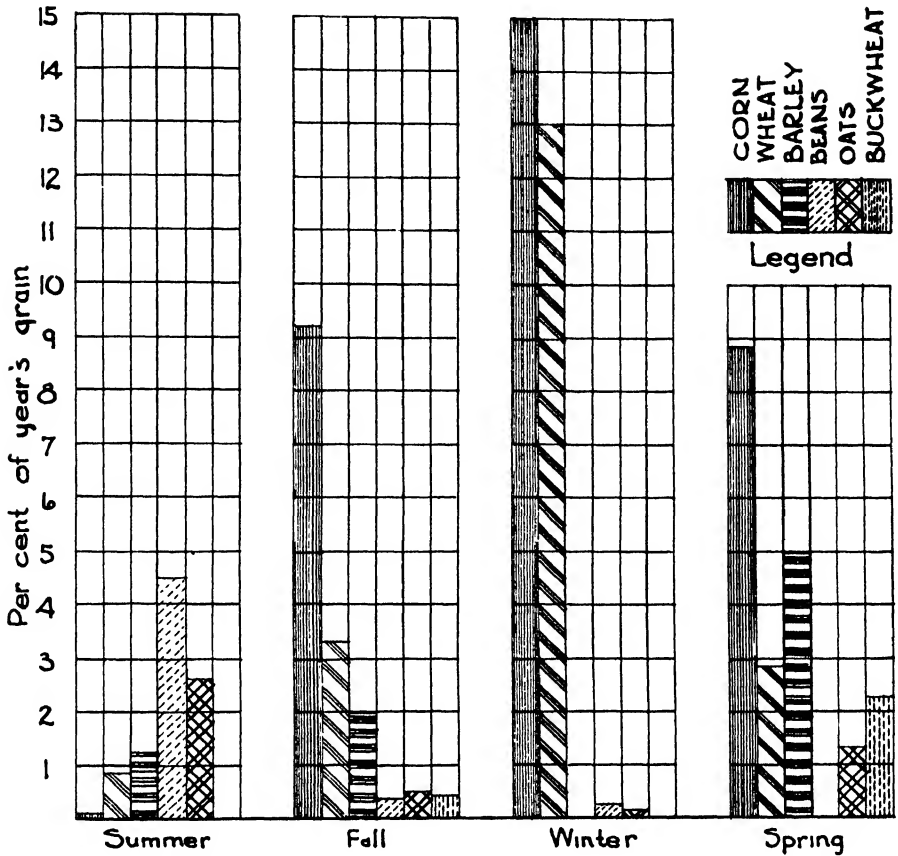


FIG. 3. Seasonal fluctuations of the cultivated grains eaten by adult pheasants. Percentages based upon the total grain of the year.

are shown in table VII. February was the only month in which no animal food was found.⁵

TABLE VII. *Percentage of plant and animal food eaten by adult pheasants for each month of the year*

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Plant....	96.4	100.0	99.9	95.9	98.5	86.8	91.7	97.9	96.1	98.1	99.8	99.9
Animal..	3.6	0.0	0.1	4.1	1.5	13.2	8.3	2.1	3.9	1.9	0.2	0.1

The percentage of plant food eaten each month is so high that the animal food is overshadowed. Their partiality to cultivated grains during all seasons

⁵ Several crops were collected after these data were assembled and the larvae of the March fly, *Bibio* sp., were found in two instances and one ladybird beetle was taken from a third crop.

of the year indicates that pheasants in Michigan are essentially farm-game birds, rather than birds of the border line agricultural communities.

WILD SEEDS AND FRUITS EATEN BY ADULT PHEASANTS

The July crop analyses indicate that no wild seeds are consumed during that month. Since the number of crops for July is hardly a fair sample, the examination of gizzards and droppings reveal, however, that although the quantity of wild seeds^a fed upon was small, nevertheless ten different species were eaten.

Neither did wild fruits appear in the crop analyses, but raspberries and immature fruits of panicle dogwood were found in droppings and gizzards of pheasants in July.

Pheasants in areas where there are large raspberry thickets fed extensively upon these fruits. Droppings collected from birds feeding in raspberry thickets were colored a light pink for a period of two to three weeks, and the seeds were consistently found in the feces, showing that raspberries were being eaten continually. Cherry pits of the wild black cherry (*Prunus serotina*) were frequently found in July droppings. Pheasants have also been observed occasionally eating cultivated cherries from the ground.

Leaves and grass made up 7.2 per cent of the food for July and consisted for the most part of alfalfa and clover leaves. Direct observations upon pheasants indicate that there is, on the part of some pheasants, a distinct preference for wild lettuce over clover or alfalfa.

Beginning in the latter part of August, various species of seeds and fruits become available and are consumed in increasing amounts. Yellow (*Setaria glauca*) and green (*Setaria viridis*) foxtail are among the late summer favorites, while ragweed which begins to mature in September formed 3.6 per cent of the month's food. It assumed an important part of the seed diet from that time until the end of March. The period of abundance for yellow and green foxtail is comparatively short. They reach their maximum in September, when they make up 9.0 per cent of the food. Yellow foxtail is found more generally over large areas of diversified farm land than is green foxtail. This accounts for the larger percentage observed in the crops. Other September seeds eaten sparingly were barnyard grass, smartweed, bur marigold, chess, and prickly ash. Fruits and nuts, although still rather unimportant at that season, form 4.2 per cent of the month's food.

The variety of plant food reached a maximum in October. At that time a total of 47 species were eaten. Although many species of plants were available, pheasants preferred the cultivated grains, and the principal seed species remained nearly the same as for September.

Odd items of food which appear in October may have been due to some disturbance such as hunting. Pheasants forced to remain under cover during

^a The principal species referred to here are the yellow and green foxtail, the two species of wild grasses most attractive to pheasants in southern Michigan.

feeding periods will vary their normal diet by selecting foods ordinarily not eaten. For instance, the small seeds of the common pigweed (*Chenopodium album*) were found in 2 out of 182 crops, yet it comprised 1.0 per cent for the month.

TABLE VIII. Percentages of the more important wild seeds eaten by adult pheasants based upon crop analysis

	Per cent of total year's food	Per cent of total quantity of seeds eaten
Ragweed (<i>Ambrosia artemisiifolia</i>)	6.3	51.4
Hog peanut (<i>Amphicarpa monoica</i>)	1.6	12.9
Yellow foxtail (<i>Setaria glauca</i>)	1.1	8.8
Skunk cabbage (<i>Symplocarpus foetidus</i>)	1.0	8.2
Green foxtail (<i>Setaria viridis</i>)	0.9	7.5
Black bindweed (<i>Polygonum convolvulus</i>)	0.5	3.0

By October, all wild fruits have ripened and are usually still retained on the vines and shrubs. Among the more important species are frost grape, panicled dogwood, and nightshade. Others of minor importance are hawthorne, elderberry, ground cherry, and poison ivy. Although fruits and nuts are readily available, they formed only 11.6 per cent of the month's food.

During November, a rapid increase in the consumption of wild weeds, fruits, and nuts was noted. The maximum consumption occurred in that month, amounting to 41.6 per cent of all the food. Of all wild seeds available in southern Michigan, ragweed seems to be the pheasants' first choice. Stubble fields of wheat, oats, barley, rye, and corn are its ideal habitats. Its wide distribution, abundance, and accessibility make it a most important food other than the cultivated grains.

TABLE IX. Percentages of the more important fruits eaten by adult pheasants, based upon crop analysis

	Per cent of total of year's food	Per cent of total amount of fruits eaten
Frost grape (<i>Vitis vulpina</i>)	4.1	54.3
Panicled dogwood (<i>Cornus paniculata</i>)	0.4	5.3
Nightshade (<i>Solanum dulcamara</i>)	0.3	3.9
Elderberry (<i>Sambucus canadensis</i>)	0.2	2.8

The importance of fruits during periods of deep snow is readily seen by the increased proportion of frost grape in the diet of pheasants during November, after the first snow storm has occurred, and also by numerous direct observations of birds feeding on grapes and nightshade. Pheasants tend to frequent shrub areas and thickets during such weather and are consequently more closely associated than usual with the wild fruits, particularly frost grape. In certain areas where frost grape was abundant, pheasants were observed feeding upon this source of food almost to the exclusion of

other nearby foods such as ragweed and burdock. Black chokeberry is known to have repeatedly wintered over a flock of pheasants in an otherwise unproductive food area.

The percentage of wild seeds declined sharply in December to 18.7 per cent. Ragweed and black bindweed (*Polygonum convolvulus*) were commonly eaten. Pheasants collected in stubble fields had fed extensively at times upon the black bindweed. The speckled beans of the hog peanut (*Amphicarpa monoica*) were eaten consistently in small quantities in areas where this plant is common. During December only 12 species of seeds were recorded in the crop analyses. Tracking in the snow brought the total of all seed species eaten up to twenty-nine. This is especially interesting in view of the logical assumption that some foods may be so completely digested as to be indistinguishable in the droppings.

The low percentage of wild seeds eaten during January may be explained by the fact that at the various times when the fifteen pheasants were collected, snow was either on the ground or the birds were collected in areas where the grain fields had been thoroughly pastured. Wild fruits, especially frost grape, were consumed to the amount of 45.7 per cent of the month's food.

The number of weed seed species in crops during February showed a marked decline over January. This may be partly accounted for by the presence of snow on the ground and the smaller number of crops examined for this month. The February birds were collected in 1932 and 1933 in an area where the total snow for this month was 6.0 and 8.7 inches, respectively, whereas in January it was only 0.5 and 0.8 inches. Fecal analysis indicates that the following species, other than ragweed, were eaten in moderate amounts: black bindweed, pigweed, smartweed, frost grape, and panicked dogwood. Tracking in the snow indicated that the two latter species were eaten whenever available. The snow under grape and dogwood thickets was often packed hard through continual use by pheasants.

During March, grass and leaves played an important rôle as a pheasant food, amounting to 10.7 per cent of the total.

The sudden increase in the amounts of grass and leaves eaten by pheasants in late winter cannot be adequately explained on the basis of availability. Pheasants are within the breeding season by March and this increase in green food may be very likely a seasonal dietetic requirement associated with reproduction. Frost grape was still available and where flocks were not broken up, the birds were observed feeding regularly upon the remnants of this fruit. The chief seed species eaten was skunk cabbage. The small amount of ragweed found in the crops for March represents the last of the easily available supply. In April, as in March, the chief seed species found in the crops was skunk cabbage. Although skunk cabbage was present in sufficient quantity by dry weight to make it appear important, it is not widely distributed. The high percentage in this case appears to be only a chance occurrence.

The percentage of wild seeds for May does not represent a good average because a single pheasant apparently had found a place where the hog peanut was still plentiful and had filled up on it. The seeds comprised 17.0 per cent of the month's food.

In June when adult pheasants are more insectivorous in their feeding habits than in any other month of the year, even the early ripening seeds are not overlooked. The seeds of the common chickweed (*Cerastium vulgatum*) and cleavers (*Galium Aparine*) are eaten in small quantities.

From the foregoing discussion of plant foods, one point stands out conspicuously. The pheasant finds satisfactory food in a great variety of plants and among these the kind of food eaten at any time depends primarily upon its availability, rather than the species.

ANIMAL FOOD

The quantity of animal food consumed by peasants during a year's time amounts to only 3.2 per cent of the total food eaten—an item which appears rather unimportant compared to the plant foods consumed. Of all the animal food taken, insects comprise by far the largest proportion. The percentage distribution of these animals is shown in table X.

TABLE X. *Percentage distribution by months of insects eaten by adult pheasants*

Order	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Lepidoptera	0.0	0.0	0.0	trace	0.2	10.1	8.2	0.1	1.1	trace	trace	0.0
Diptera	3.6	0.0	0.0	trace	0.1	0.0	trace	0.0	0.0	trace	trace	trace
Coleoptera	0.0	0.0	trace	1.2	0.3	3.0	0.0	trace	0.1	trace	trace	trace
Hymenoptera	0.0	0.0	trace	0.0	0.0	trace	0.0	0.0	trace	0.0	0.0	0.0
Hemiptera	0.0	0.0	0.0	trace	trace	0.0	0.0	0.0	0.0	trace	trace	0.0
Homoptera	0.0	0.0	0.0	trace	trace	0.0	0.0	0.0	0.0	trace	0.0	0.0
Orthoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	2.7	1.8	0.2	0.0
Unidentified	0.0	0.0	0.0	0.0	0.0	trace	0.0	0.0	0.0	0.0	0.0	0.0
Totals	3.6	0.0	trace	1.2	0.7	13.1	8.2	1.9	3.9	1.8	0.2	trace

During the summer months the insect consumption was at its highest point, the peak coming in June, the period of maximum insect activity. The diet at this time of year was comprised of 13.1 per cent insects, most of which were the larvae of Lepidoptera. In July, the insect food was mostly Lepidoptera. Although insects are available in abundance in the summer, adult pheasants do not utilize them as their principal source of food. The graph in figure 2 indicates clearly just how small a portion of the year's food is animal matter. The peak of grasshopper consumption came in September and dropped to almost nothing by the end of October. During mild open winters, pheasants may be expected to feed upon the larvae of the March Fly, *Bibio* sp. The larvae of this insect are gregarious and hibernate in the litter in shrub thickets.

The larvae were eaten during January to the amount of 3.5 per cent of the month's food.

TABLE XI. *Percentages of insects, by orders, eaten by adult pheasants*

Order	Per cent of year's food	Per cent of insect food eaten
Lepidoptera	1.6	56.9
Orthoptera	0.6	19.0
Coleoptera	0.4	13.1
Diptera	0.3	10.6
Hemiptera	trace	0.2
Hymenoptera	trace	trace
Homoptera	trace	trace

The relative importance of the various orders of insects is seen in the above table. Lepidoptera, all in larvae stages, rank first in quantity of insect food eaten. The common belief that grasshoppers are consumed in large quantities by pheasants is not borne out by this investigation. Orthoptera including both locusts and field crickets, amount to only 0.6 per cent of the year's food, and only 19.0 per cent of all insect food eaten.

The largest amount of animal food consumed other than insects occurred in April. In this month, the land snail, *Polygra* sp., comprised 2.8 per cent of the food. In addition to snails, sow bugs (*Oniscus* sp.), millipedes, and spiders were found in small quantities. Of all the animals eaten by pheasants other than insects, the mollusca were most important.

SUMMARY

1. Pheasants feed little during the middle of the day, summer or winter.
2. The crop is not always full when the bird goes to roost, even though food is abundant. Approximately 14 per cent of the pheasants collected at sundown had full crops. In all cases, however, other parts of the digestive systems were full of food.
3. Habits of feeding are not uniform but are very regular with certain flocks. Areas of wild fruits are completely utilized by daily feeding throughout late fall and winter.
4. The pheasant is an omnivorous feeder; the greatest variety of seeds and fruits eaten occurred in October when 106 species were recorded.
5. The high percentage of grain eaten by pheasants is not an indication of damage to grain crops. Most of the grain consumed is waste, either from harvesting or planting, or from manure spread on the fields. Corn, wheat, and barley comprise 83 per cent of all the grain eaten.
6. In the pheasant territory of Michigan, the most common wild seeds eaten were ragweed, yellow foxtail, skunk cabbage, and green foxtail. Ragweed accounted for 51 per cent of all the seeds eaten. Wild fruits and nuts are eaten consistently, but their percentage is small (7.48), since the habitat of

these species are restricted to a relatively small proportion of the pheasant range.

7. Adult pheasants are not large consumers of insects and other invertebrates in comparison with plant food eaten. The common belief that grasshoppers are consumed in large quantities is not borne out by the investigation.

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ASSOCIATION TYPES IN THE NORTH COAST RANGES OF CALIFORNIA

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The north coast ranges of California occupy the territory extending from San Francisco Bay northward to Humboldt and Trinity counties, and from the Sacramento Valley to the Pacific Ocean. This region comprises a strip of rugged mountain terrain whose climatic, vegetational, and faunal features are exceedingly diversified, and extremely difficult to interpret. Merriam (1898) recognized this region as the most complex in the United States. Harshberger ('11) referred to the great variety of plant and animal life in Mendocino and Lake counties. Others have commented on the problems involved in the proximity of coastal and interior types, among whom are W. K. Fisher ('00) and Witmer Stone ('04).

BIOGEOGRAPHICAL AREAS

The mountains of this region may be divided into two main portions. The outer range follows the coast in a series of ridges from 1500 to 4000 feet high. East of them lies a rough area of broken ridges and valleys, on the eastern edge of which the inner coast ranges border the Sacramento Valley in an almost unbroken line 2000 to 6000 feet high. The contours of the ranges profoundly modify the course of the prevailing winds, bringing about variations in temperature, rainfall, humidity, and wind velocity. These variations are reflected in the distribution of plant and animal life (fig. 1).

In a consideration of the vegetation of the region, we find it natural to recognize four distinct divisions of the territory, each with its characteristic species and climatic features. These divisions might be called "biotic areas," and they correspond closely to Grinnell's "faunal districts" (Grinnell, '15).

The area between the outer coast range and the ocean is known as the humid coast belt. It is a region of uniform temperature, high humidity, and abundant rainfall. These factors make it one of luxuriant growth. The valleys near the coast support forests of magnificent redwood, *Sequoia sempervirens*, and the hills are clothed with Douglas fir, *Pseudotsuga taxifolia*, mingled with tan oak, *Lithocarpus densiflora*. Along the river flats the California laurel, *Umbellularia californica*, and lowland fir, *Abies grandis*, are scattered through the redwood forests. Many species of shrubs form a dense understory and often occur in solid masses, while the forest floor is covered with shade-loving herbs.

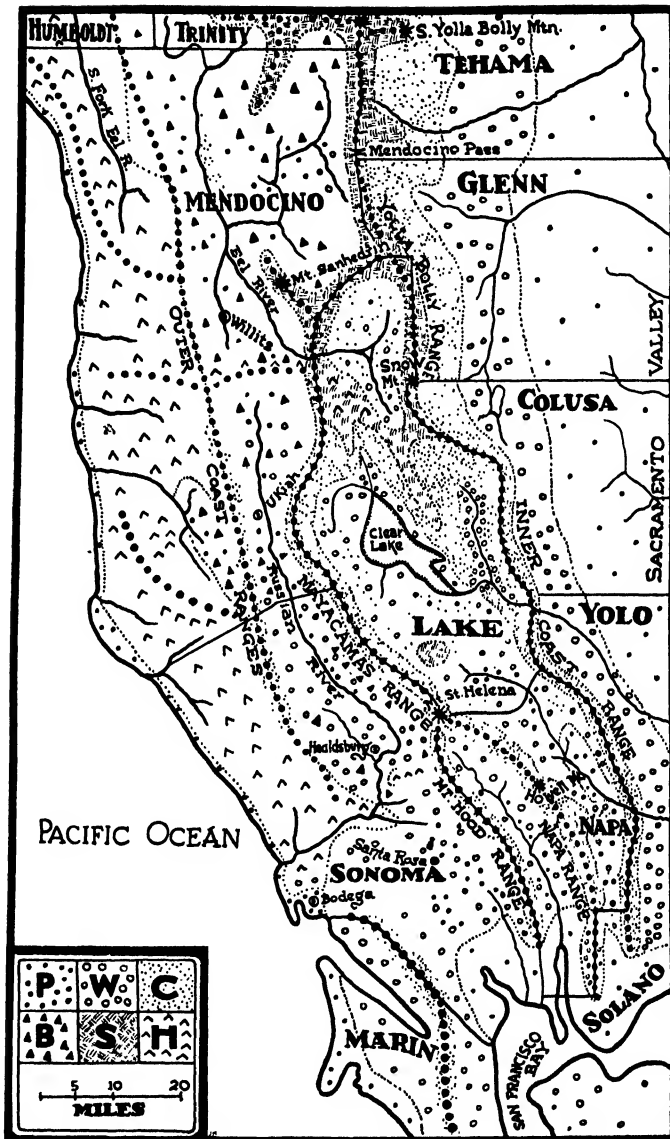


FIG. 1. Map of a portion of northwestern California, showing area covered by this paper. Symbols: P, prairie; W, woodland; C, chaparral; B, bald hills region, with woodland and prairie; S, sierran montane forest; H, humid coast region.

Humid conditions prevail to the summits of the outer ranges, but here the strong winds often prevent heavy growth, and the "bald hills" develop grassland instead of forest. Open grassland also occurs close to the shore, forming a belt from a few hundred feet to two or three miles wide between the

sea bluffs and the forest. This is often mingled with low brush in scattered localities, or with straggling patches of Bishop pine, *Pinus muricata*, beach pine, *Pinus contorta*, lowland fir, Douglas fir, and redwood. Occasional patches of Sitka spruce, *Picea sitchensis*, will be found from the middle of Sonoma county northward.

That portion of the humid coast belt north of the mouth of the Russian River might be designated as the Humboldt Biotic Area. The portion between the Russian River and San Francisco Bay, eastward to the Napa Range, constitutes the San Francisco Biotic Area. The predominance of coniferous forests, with the presence of distinctly northern types such as the Sitka spruce, differentiates the northern portion from the southern, which is characterized by more southern types such as the coast live oak, *Quercus agrifolia*.

North of the Russian-Eel River divide, and east of the humid coast belt, lies another distinct region, the Trinity Mountain Biotic Area. For an interpretation of this area we go to the Yolla Bolly Mountains, where the inner coast ranges find their climax. From the vicinity of South Yolla Bolly (8604 feet) high ridges run northward through North Yolla Bolly and into the Bully Choop, Trinity, and South Fork mountains. There is also an extension westward to the Eel River. Southward the ridge extends at an approximate elevation of 6000 feet to Snow Mountain at the corners of Lake, Glenn, and Colusa counties. From here broken mountain masses run south and west into Lake and Napa counties.

The Yolla Bolly range is an area of rugged ridges and deep canyons, with few open valleys. The higher portions are clothed with a forest resembling that of the middle altitudes of the Sierras, with patches of snowbrush, *Ceanothus cordulatus*, bitter cherry, *Prunus emarginata*, Brewer oak, *Quercus garryana breweri*, and huckleberry oak, *Q. vacciniifolia*. Below the forest belt on the east side, where the slope drops abruptly into the Sacramento Valley, lies a strip of chaparral, below which is the savanna and open prairie region.

Between the main range of the Yolla Bolly's and the South Fork of the Eel River lie a series of ridges from 2000 to 5000 feet high. The summits of the highest are covered with brush of the species just mentioned. More moderate elevations support heavy woodland of Garry oak, *Quercus garryana*, mixed with Douglas fir. Below 4000 feet is found the best development of the "bald hills" grassland, while the more abrupt ridges may show large masses of chaparral species common to more southerly regions. The ravines and moderately steep slopes often have an open woodland of Garry oak and madrone, *Arbutus menziesii*.

West of the South Fork of the Eel River the tan oak, *Lithocarpus densiflora*, becomes a prominent feature, forming a "distinct belt just inside the Redwood Belt" (Jepson, '10), where it mingles with the Douglas fir from the humid coast belt and the Garry oak and madrone from the bald hills country. Patches of this mixed hardwood and coniferous forest extend for some dis-

tance eastward on the more abrupt north-facing slopes. In the deep canyons the canyon live oak, *Quercus chrysolepis*, grows to magnificent proportions, and large numbers of shrubs line the canyon walls.

Ukiah Valley in Mendocino County, Napa County east of the Napa Range, and practically all of Lake County below 5000 feet elevation, constitute a semi-arid area shut off from the sea by the Napa and other ranges to the north and northwest. In general floristic aspects this region appears like the foothills of the Sierras rather than like the lower portions of the Sacramento Valley, and because of its dissimilarity with the valley should justifiably be considered a separate area, the Clear Lake Biotic Area (fig. 1).

The principal tree species of this area are the blue oak, *Quercus douglasii*, interior live oak, *Quercus wislizenii*, and digger pine, *Pinus sabiniana*. The hills are commonly covered with chaparral, the chief species being chamise, *Adenostoma fasciculatum*, leather oak, *Quercus durata*, white-leaf manzanita, *Arctostaphylos viscida*, toyon, *Photinia arbutifolia*, coffee berry, *Rhamnus californica*, silk tassel bush, *Garrya elliptica*, and mountain mahogany, *Cercocarpus betuloides*.

CLIMATIC TYPES

The region between the outer coast ranges and the Sacramento Valley, even though shut in by high ridges, is considerably tempered by winds from the northwest. This is especially noticeable in June, due to the warming up of the Sierras, and the consequent movement of air inland. The elevation of the Trinity and Yolla Bolly ranges deflects these currents southward, and is one of the main factors in maintaining the semi-desert conditions of the upper end of the Sacramento Valley as well as tempering the valleys in the north coast region.

Another important factor in the summer climate of the north coast valleys is the downward drainage from the mountains surrounding them. The effect is to cool the valleys during the early morning hours. By time the heat of the day comes on, cooling breezes usually come in from the coast, drawing up the valleys and through low gaps in the ranges. The midday temperatures are much more moderate in the coast valleys than in the Great Valley.

Four types of climate have been recognized by Russell ('26): (1) *Hot valley climate*, in the Sacramento and tributary valleys; (2) *Cool valley climate*, in the valleys and mountains west of the Napa-Mayacamas range, below 2500 feet; (3) *Cool mountain climate*, on the summits of the outer coast ranges except close to the ocean, and on the inner ranges above 2500 feet; and (4) *Fog-belt climate*, on the lower slope of seaward side of the outer ranges. Summers are long in all but the cool mountain climate, and cool in all but the hot valley climate.

The climate of the high mountains is peculiar. The season begins late, but the temperature curve rises rapidly, and by midsummer the temperatures are on the average higher than at corresponding elevations in the Sierras.

Currents of heated air from both sides of the Yolla Bolly Range meet at the summit, and severe electrical storms are of frequent occurrence during the summer.

The steep slopes of the Yolla Bolly Range do not cool the air as much as do the long west slopes of the Sierras. As a result, certain zonal indicators are found at approximately 1000 feet higher than in the Lassen region fifty miles away, across the Sacramento Valley.

The rainfall comes largely during December, January, and February with occasional heavy storms as late as April or May in the northern portion. The northwest winds in northern Lake and Mendocino counties in late spring and summer tend to increase the total precipitation by causing the condensation of moisture about the mountains. Storms of short duration occur here after the rains have ceased farther south. In midsummer the heated currents which produce thunderstorms may not add to the total precipitation appreciably, but the effect is to lessen the amount of evaporation, and to temper the sun's rays during the middle of the day. All these factors have their effect upon the distribution of vegetation.

BIOTIC ASSOCIATIONS

A fundamental principle regarding the relation between plants and animals in a community was enunciated by Vestal ('14), when he contended that the two formed a community that might be termed a "biotic association." Clements, in dealing with plant ecology, says ('20) that the animals must be considered an intrinsic part of the community. Nicholson states ('31) that avifauna and flora are to be considered together. In his system he bases the grouping of bird habitats on vegetation units. This is in harmony with the methods followed in Europe and suggested by some American workers (Shelford, '13, Svihla, '32). Phillips ('31) says that the whole community must be taken together, and speaks of the biotic community as the most logical and practicable of concepts.

On the other hand, considerable objection has been raised to the views of Clements in regard to the biotic community. Tansley ('35) is outspoken in his criticism, and suggests that plants and animals are simply "components" of an "ecosystem," which takes into account all the organic and inorganic factors of the environment. Braun-Blanquet ('32) maintains similar ideas, and builds up a system of plant sociology that takes into account both the floristic and ecologic relations of the association.

In studying the distribution of plant and animal life in the north coast ranges of California, I have tried to profit by the various viewpoints, and to find a simple, yet comprehensive method of designating the ecological units. I have found an adaptation of Schimper's system (Schimper, '03) to be the most practicable. This system is based on vegetational units. Four groups of associations can be recognized, corresponding to the "formations" of

some plant ecologists, or to the "associations of major rank" of Grinnell and Swarth ('13). Under these I have designated six "association types." These correspond roughly to the "associations" of Grinnell and Storer ('24), or to the "habitats" of Grinnell, Dixon, and Linsdale ('30). It would be easy, following this system, to arrange the local associations, based on dominant floristic types, under the various association types and subtypes.

Associations have been defined (Shelford, '13) as definite biogeographical units of generally uniform conditions. The same author says ('31) that the "major community," using the term in the sense of the animals inhabiting a given association, is the unit of ecological classification. Svihla ('32) using the word "habitat" in the sense of association, says that it is the natural basis for classification. Saunders ('21) calls associations the most fundamental of distributional units, and classifies the associations of Montana in much the same way as this paper deals with those of northern California.

The use of plant associations as a basis for the classification of animal communities has been justified by Brock ('14) who says that plant associations of similar nature will have similar avifauna. Vestal ('14) says that the character of the plant population is an index to the ecological type of animal population. Weaver and Clements ('29) state that animals are an intrinsic part of the climate formations, but that they are not dominant, inasmuch as they do not respond directly to the climatic factors. Their presence or absence is determined by the plants, which are directly responsive to the environment. The use of plant indicators as keys to the distribution of associations has proved successful (Braun-Blanquet, '32), and has been used widely by Hall and Grinnell ('19) and other workers.

In accordance with the foregoing principles and usages, I have taken the plants as the basis for the classification of biotic communities, and have designated the principal association types to be found in the territory under study. In order to allow for minor differences in distribution which are apparent in a territory of great complexity, it has been necessary to recognize "subtypes," based on the distribution of floristic rather than ecological forms. In this I have been influenced largely by the unpublished work of the California Forest Experimental Station at Berkeley.

ASSOCIATION TYPES

A. Associations in which grassland species predominate

1. *Prairie Association Type*

The grasslands of California are not to be classed as prairie as the term is applied in the middle west. The open grasslands of the interior valleys of California are most closely related ecologically to the tropical savanna-steppes, there being an almost imperceptible gradation between the temperate and tropical types (Bews '29). According to Schimper ('03), tropical

grasslands develop where the warm and rainy seasons coincide, in contrast to temperate grasslands which are found where the winters are too dry for tree growth. The low valleys of California are without analogy in either the temperate or tropical belts. They are too hot and dry in summer to allow temperate prairie grasses to grow; the winters are warm enough to allow some of the tropical types to grow; so they might be classed as subtropical, approaching more closely to the tropical grasslands of South America and Africa than do the grasslands of any other part of North America, Europe, or Asia (Bews, '29).



FIG. 2. Open grassland bordered by foothill woodland on the west slope of Snow Mountain, at 3500 feet, with chaparral behind and a fringe of yellow pine forest at 4500 feet.

From San Francisco Bay northward on the west slopes of the outer and middle coast ranges, and in the Yolla Bolly region, are found open grassy areas, locally known to sheepmen as "glades." At first these appear to be merely extensions of the valley grassland over the hill slopes, due to drying winds and intense afternoon sunshine; but as one goes farther north he finds these open areas increasing in size and running lower into the valleys. From the corner of Mendocino and Trinity counties northward into Oregon and Washington they form large areas of temperate grassland, much like true prairies in character, with bromes and fescues replacing the stipas and poas of the California valley grasslands. These temperate grasslands have been called "bald hills" (Jepson, '10) in California, "hill prairie" (Lawrence, '26) in Oregon, and "gravelly prairie" (Piper, '06) in Washington (fig. 2).

According to Davy ('02) perennial grasses are more abundant on the coastal strip, with many boreal species of herbaceous plants and shrubs.

Three subtypes of the prairie association may be distinguished:

a. Savanna Prairie, found mostly in the Sacramento Valley and in the low, hot valleys of the inner coast ranges. This closely approaches the semi-desert or tropical savanna steppes in ecological nature. The grasses are low, and of short duration. Valley oak, *Quercus lobata*, occurs in scattered stands of large trees. The coast live oak is found in connection with valley oak in the San Francisco Biotic Area and the interior live oak in the Sacramento Valley.

b. Hill Prairie, comprising the open hill grasslands previously mentioned (fig. 5).

c. Coastal Prairie, occupying the coastal strip between the humid coast forests and the ocean shore. This is similar to hill prairie in nature, but with a much larger assemblage of herbaceous plants and low shrubs.

2. Meadow Association Type

True boreal meadow is exceedingly rare in the coast ranges of California. Even in the Yolla Bolly Mountains, where red fir forests are present, the low areas are limited in extent, summer moisture is scarce, and midsummer temperatures are high. The conditions more closely resemble those prevailing in the mountains of southern California than in the Sierras, and the meadows are more of the nature of marshes than of true meadows. The term "cienaga" (marsh), used by Grinnell ('08), in reference to the mountain meadows of the San Bernardino mountains is, possibly, more expressive of the conditions than the word *meadow*.

Two subtypes of the meadow association are to be noticed:

a. Valley Meadow, found in a few scattered localities, such as at the upper end of Clear Lake, or at the lower end of the ancient crater on Howell Mountain. This subtype is largely of a seasonal nature, being marshy in winter and dry in summer. Cultivation has obliterated nearly all the original meadow land.

b. Boreal Meadow, of very infrequent occurrence in the Yolla Bolly Mountains above 5000 feet, and along the coast from Mendocino County northward. The soil in the Boreal Meadow is rich and deep, sometimes boggy or marshy. Characteristic plant indicators are the skunk cabbage, *Lysichiton kamschatcense*, false hellebore, *Veratrum californicum*, and forget-me-not, *Myosotis sylvatica*. Various species of willows border the meadows. On the coast red alder, *Alnus rubra*, is common along the edges of meadows, but is replaced by mountain alder, *Alnus tenuifolia*, in the mountains.

B. Associations in which chaparral and hardwood species predominate

3. *Chaparral Association Type*

The interpretation of the scrub lands of California is extremely difficult. Much study has been given to the problem of their classification, but detailed reports are scarce, and viewpoints differ widely. Jepson ('25), Plummer ('11), Clements ('20), Grinnell and Swarth ('13), Harshberger ('11), Abrams ('10), Grinnell, Dixon, and Linsdale ('30), and the California Forest Experiment Station each has his own way of classification. The only claim which I can make for my own classification is that it is closely related to that being followed by the latter group of workers, with, however, a fuller recognition of the ecological problems than they include in their system. The stricter ecological viewpoint is based more on the principles brought out by Clements ('20) and Cooper ('22).

The following division of the chaparral into three subtypes seem to me to be the simplest and most nearly in harmony with the climatic and other ecological factors that are evident as one studies the region:

a. Low Chaparral, found on steep rocky ridges, especially on the tops and west slopes of all ranges south of Snow Mountain and east of the humid coast belt, on the east slopes of the Yolla Bolly Mountains from 1000 to 3000 feet, and in scattered areas along the Eel River into Trinity County. Ecologically this subtype corresponds to the hard, or true chaparral of Jepson and Plummer. The principal species are chamise, leather oak, white-leaf manzanita, toyon, coffee berry, silk tassel bush, mountain mahogany, and digger pine. These grow from three to six feet high (except the pine) in open stand, or may run into close formation as this subtype blends into the next.

b. High Chaparral, found in canyons and ravines, along sea bluffs, or on exposed hills of the coastal belt; scattered on the cooler slopes of the Napa, Mt. Hood, or Mayacamas ranges, and on the lower slopes of ranges in southern Lake and Mendocino counties. The high chaparral grows from six to fifteen feet high, and some kinds are tree-like in size and growth habit. The most important species are scrub forms of the interior live oak, coast live oak, and canyon live oak, with a mixture of leather oak, laurel, wild lilac (*Ceanothus* spp.), buck brush, *Ceanothus cuneatus*, coyote brush, *Baccharis pilularis*, sticky monkey flower, *Diplacus glutinosus*, and several species common to the low chaparral.

c. Forest Chaparral, found above 5000 feet on the Yolla Bolly Mountains and connecting ridges. This brushland most generally occurs in small patches scattered throughout the forest or in solid stands on exposed ridges. The dominant species are snowbrush, bitter cherry, Brewer oak, scrubby Garry oak, and huckleberry oak (fig. 3).



FIG. 3. Forest chaparral on Snow Mountain, at 6500 feet, Brewer oak and bitter cherry in the foreground, huckleberry oak in the center and snowbush to the right.

4. *Woodland Association Type*

Terminology of the woodland is confused, embracing such terms as "savannah," "shrub savannah," "encinal," "oak-covered hills," "blue oak country," etc. The term woodland is used by the United States Forest Service to distinguish the forests of low, arid hills from the montane forests, which are mainly coniferous. Many of the woodland species run into chaparral with no distinct line.

According to Schimper ('03), while grasses must have a moist superficial soil, trees depend on a moist subsoil and suffer more from low humidity than do grasses. The savannas are characterized by those perennial bunch grasses which are able to survive long dry seasons and those trees which can endure extremes of humidity. Warming ('25) says that typical savanna undergoes its resting period during the dry season, which is the cold part of the year.

The California valleys approximate these conditions sufficiently to develop an open wooded area resembling a true savanna, and over the foothills of the Sierras and rolling hills of the coast ranges is found a stable combination of grasses and scattered trees that to all appearance and in ecological relation is a savanna.

While extremes of summer and winter climates occur, the woodland consists of deciduous trees (Salisbury, '26). The sclerophyllous woodland is found in climates where the winters are mild and moist and the summers dry; when this condition becomes extreme, the woodland gives way to chaparral. Woodland areas are invading bare areas in the north coast ranges (Jepson, '10), and are often successional, leading to montane forest (Clements, '20).

Although peculiarities in the distribution of certain species of trees in the woodland might make it seem almost necessary to recognize several subtypes, I have, for the sake of simplicity, designated only three, as follows:

a. *Foothill Woodland*, occurring on foothills and moderately steep slopes up to 4000 feet, north to the Russian-Eel River divide; also in scattered valleys in northern Lake and eastern Mendocino counties. This woodland consists of mixed stands of coast live oak, blue oak, black oak, *Quercus kelloggii*, interior live oak, madrone, laurel, digger pine, and buckeye, *Aesculus californica*, in varying proportions. The growth is dense and thicket like, or partly open. The trees grow from six inches to two feet in diameter, and from fifteen to fifty feet high. The ground is sometimes partly covered with grass, or may be almost entirely covered with litter. Chaparral shrubs occasionally mingle with true woodland species.

b. *Bald Hills Woodland*, occurring on the hills east of the South Fork of the Eel River and eastward to the Yolla Bolly Mountains, thence northward into Humboldt and Trinity counties; also on the west slopes of the Yolla Bolly Range near Mendocino Pass, on the west side of Snow Mountain, and in the vicinity of Healdsburg and Clear Lake, and in scattered areas on the west slope of the outer coast range.

The region supporting this subtype is one of moderate climate, with cool, late summers as compared with the region to the southward. From a distance the bald hills have a superficial resemblance to the savannas of the valleys near the Bay, but closer examinations reveal the fact that whereas in the savannas the trees and grass form a balanced mixture, in the bald hills one or the other is dominant.

At elevations of from 3000 to 5000 feet this type runs into magnificent woodlands and mixes with the forests of the mountains to the east and the humid coast belt to the west. The Garry oak reaches its best development on the high hills of this region, forming open woodlands of large trees, widely spreading, and with no undergrowth.

Besides Garry oak, the woodlands in this area contain a large admixture of black oak, interior live oak, canyon live oak, big-leaf maple, *Acer macrophyllum*, buckeye, and Parry manzanita, *Arctostaphylos manzanita*. These may grow in open formation, in thickets, or in solid growth resembling forest.

c. *Streamside Woodland*, occurring along streams or lake shores, and in moist valleys up to 5000 feet. As a general rule cottonwood, *Populus fremontii*, thrives in the lower and hotter portions of the region, valley oak in the more temperate portions, and alders in the cooler and more humid portions. The irregularities of topography make it impossible to apply this rule rigidly. In open or chaparral areas there is a sharp separation between the streamside woodland and nearby associations, but in areas of foothill woodland or forest associations there is a blending of biotic elements. Often in broad valleys the valley oak or Garry oak may form dense thickets of slender

trees along the streams and groves of giant trees with rounded tops in the open bottom lands.

In the narrow strip close to the coast the red alder replaces the white alder, *Alnus rhombifolia*, which is common along mountain streams. The stream-side association in deep canyons in the humid coast belt often forms a mixture with the forest. Inasmuch as redwood and laurel grow on moist flats, the alder may form only a narrow fringe along the stream.

In the canyons of the higher mountains the creek dogwood, *Cornus californica*, and mountain alder may be overshadowed by the surrounding forest, but in boreal meadows and in wet spots on the margin of the forest, dense thickets occur. Several species of willow also occur throughout the region. Grass and herbage grow close to the streams, and typical marshy areas may occasionally develop where areas of flat ground become saturated from the stream.

Often a rank growth of shrubs and vines may take place as an understory to the dominant species. The most important of these forms are ninebark, *Physocarpus capitatus*, snowberry, *Symphoricarpus racemosus*, California blackberry, *Rubus vitifolius*, California grape, *Vitis californica*, and coyote brush.

C. Associations in which coniferous species predominate

5. Sierran Montane Forest Association Type

The Sierran montane forest described by Clements ('20) for the Sierra Nevada region extends around the head of the Sacramento Valley and down the ranges bordering that valley on the west. Although not so well developed as in the Sierras, the forests of the Trinity and Yolla Bolly mountains contain most of the representative species of plants and animals, and are more closely allied to the Sierran type than to the Douglas fir and redwood forests of the northwestern region.

The scattered yellow pine forests south of Snow Mountain are so surrounded and mixed with other types that clear distinctions are difficult. They occupy a region of moderately high humidity, warm summers, cool winters, and fairly good soil. In California the area where conditions are favorable for the development of this type of mixed forest is so limited in extent that it does not become a dominant type, and must be regarded instead as a mixture of other types which in this region do become dominant.

The dominant species found in the higher mountains of the north coast ranges are western yellow pine, *Pinus ponderosa*, sugar pine, *P. lambertiana*, incense cedar, *Libocedrus decurrens*, white fir, *Abies concolor*, and red fir, *A. magnifica*. Other important species are Douglas fir, black oak, green manzanita, *Arctostaphylos patula*, white-leaf manzanita, and blue brush, *Ceanothus soledatus* (fig. 4).



FIG. 4. Plaskett Meadow and Black Butte, Yolla Bolly Range, with boreal meadow in foreground surrounded by Jeffrey pine, white fir and red fir, constituents of the Sierran montane forest.

Two subtypes must be recognized, although very poorly developed in the coast ranges. A study of the forests of the Sierras indicates, however, that the Sierran forests of the north coast mountains contain fragments of the following subtypes:

a. Yellow Pine Forest, forming a belt between the chaparral and the fir forests, into which the pines blend at their upper line, usually around 6000 feet.

b. Fir Forest, occurring in small patches on the higher mountaintops and on cooler slopes above 6000 feet.

On account of the poor development of these subtypes, we shall not make close distinction between their characteristic species.

6. Humid Coast Forest Association Type

The humid coast forest belt occupies the deep ravines and canyons between Bodega and the Russian River, the canyon of this river, and the western slope of the outer coast ranges except for the narrow coastal strip. Scattered patches also occur on the east slopes of the Mt. Hood and Napa ranges.

In the northern part of Lake County the high ridges running westward from the Yolla Bolly Range have a large mixture of Douglas fir that has apparently come across the Russian-Eel River divide. The presence of this tree in California is possible only where climatic conditions provide low summer temperatures (Merriam, 1898) and uniformity of temperature and moisture (Pearson, '20) (fig. 5).



FIG. 5. Scene on Eel River, showing typical humid coast forest, with small patches of hill prairie.

Three subtypes of the Humid Coast Forest must be recognized:

a. Redwood Forest, occurring on river flats and low hills near the coast. Redwood is the dominant tree, and laurel, lowland fir, and Douglas fir are common.

The redwood is probably the most restricted of any important species, living only in the "fog belt," as it cannot endure dry air, even if its roots have abundant water (Cooper, '17).

b. Tan Oak Forest, occupying the higher hills in the redwood belt, and found along the eastern edge of the redwood Forest. Tan oak and Douglas fir are the important trees of this subtype.

The tan oak belt just east of the redwood belt (Jepson, '10) becomes the dominant subtype in Mendocino and Sonoma counties, but in Humboldt and Del Norte counties the redwoods spread over the hills and are more fully developed. In these northern counties, however, the tan oak forests

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AN ECOLOGICAL STUDY OF SOME ORTHOPTERA OF THE CHICAGO AREA

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INTRODUCTION ¹

The geographical and local distribution of North American Orthoptera has received the attention of a number of capable workers. Morse ('99) demonstrated a general correlation of the distribution of New England locusts with mean annual isotherms. His conclusion (p. 320) was that the delimitation of range is "... distinctly climatal in character, although strongly influenced by physiography and its attendant conditions."

Collecting and field observations during the past three years have demonstrated an ecological succession of Orthoptera corresponding in a general way to the plant succession on the sand dunes along the southern shore of Lake Michigan. This region has been the object of ecological study since the pioneering work of Cowles in 1899. It has been hoped that a comparison of the local distribution of the species of Orthoptera with the summarized data on vegetation and the character of the physical environment in the stages of the plant succession might shed some light on the specific factors operative in the limitation of range of certain species of Orthoptera.

HISTORICAL

The species of Orthoptera occurring in Illinois and neighboring states have been treated by Thomas ('76, '80), Blatchley ('03, '20), Hancock ('11) and Hebard ('34). These works, especially those of Blatchley and Hancock, contain many notes on the gross features of the habitats of particular species.

References to Illinois and Indiana Orthoptera are to be found in many ecological papers, especially those of Hart and Gleason ('07), Shelford ('13) and Vestal ('13).

PHYSIOGRAPHY

A rather full description of the physiographical features of the region about Chicago is contained in Cowles' ('99, '01) accounts. Along the southern and southeastern shores of Lake Michigan sand deposition and wind

¹From ecological studies under the supervision of Dr. W. C. Allee. I wish also to acknowledge indebtedness to Dr. Henry Fox and Mr. M. Hebard, who gave opinions in some cases of doubtful identity of specimens of Orthoptera. Drs. G. D. Fuller and C. E. Olmsted have been of indispensable assistance in the identification of plants.

action have produced dunes of considerable height and extent; the greatest elevation is about two hundred feet above lake level. The southwestern shore of Lake Michigan lacks sand dunes of any size but many of the vegetational features are the same, particularly as regards grasses and other herbaceous plants.

The localities west of Chicago at which collecting was done, Palos Park and the Pilcher Arboretum near Joliet, lie on the Valparaiso moraine. The soil is a heavy black clay of glacial deposition. At Palos Park the usual type of forest is composed of mixed oaks or oak and hickory. That part of the Pilcher Arboretum which was visited is a forest of sugar maple, regarded as the forest climax on this soil as well as on the sand soil of the dunes.

The forest at Smith, Indiana, is on a clay soil which was covered by a deposit of sand a foot or two in depth, presumably during the Glenwood stage of Lake Chicago. The drainage is poor; part of the forest floor is sometimes under water during spring. Of the other climax forests which will be referred to that at Lakeside, Michigan, is on sandy clay while the same type of forest at Saugatuck, Michigan, is developed on the sand dunes. The necessity for considering these separately will be disclosed in the description of the vegetation and of the distribution of Orthoptera.

VEGETATION AND ORTHOPTERA

The associates recognized in the following description are those of Cowles' ('01) schematization of the ecological succession of plants in the Chicago area. Since the Orthoptera are closely associated with vegetation the most abundant and characteristic plant species of each associates will be indicated, with especial attention to those upon which these insects have been observed to feed. Fuller ('25) has prepared species lists and compact descriptions of the plant communities of the Chicago region.

1. *The Beach*. This early stage of the succession is devoid of plants except for occasional specimens of *Cakile* and *Artemisia*. While the physical factors such as light intensity, evaporation, etc., are undoubtedly similar to those of the next associates the practical absence of plants precludes the establishment of Orthoptera. Stray specimens of *Trimerotropis maritima interior* are to be found but no significance can be attached to their presence.

2. *The Fore-dune* consists of low mounds of sand from five to fifteen feet high. The dominant plant of this associates is the Marram grass, *Ammophila arenaria* Link. *Calamovilfa* also grows here and there are extensive stands of the sand cherry, *Prunus pumila* L.

Associated with the grasses are *Trimerotropis maritima interior* E. M. Walker, here approaching its western limits of distribution, *Psimidia fenestralis* Serv., and *Ageneotettix deorum* Scud. The last named is not common on the southern shore of Lake Michigan but is very abundant on the dunes at Waukegan, Illinois, which is on the western shore of the lake just north of

TABLE I. *The distribution of orthoptera in the associates of the forest succession in the Chicago area*

	Foredune	Poplar	Pine	Black oak on sand	Oak-hickory on clay	Climax, Smith, Ind.	Climax, Joliet, Ill.	Climax, Lakeside, Mich.
Blattellidae								
<i>Parcoblatta pennsylvanica</i> (DeGeer)	—	—	*	*	*	*	*	*
<i>Parcoblatta uhleriana</i> (Saussure)	—	—	—	*	*	*	—	—
<i>Parcoblatta virginica</i> (Brunner)	—	—	—	—	—	—	—	—
Phasmidae								
<i>Diapheromera femorata</i> (Say)	—	—	—	*	*	*	*	—
<i>Diapheromera blatchleyi</i> (Caudell)	—	—	—	*	*	—	—	—
Acridiidae								
<i>Tettigidea lateralis parvipennis</i> (Harris)	—	—	*	*	*	*	*	—
<i>Chloea conspersa</i> (Harris)	—	—	*	*	*	*	—	—
<i>Ageneotettix deorum</i> (Scudder)	*	*	*	—	—	—	—	—
<i>Trimerotropis maritima interior</i> (E. M. Walker)	*	*	—	—	—	—	—	—
<i>Psinidia fenestralis</i> (Serv.)	*	*	*	—	—	—	—	—
<i>Spharagemon collaris</i> (Scud.)	*	*	*	—	—	—	—	—
<i>Spharagemon bolli</i> (Scud.)	—	—	—	*	*	—	—	—
<i>Arphia sulphurea</i> (Fabricius)	—	—	*	*	*	—	—	—
<i>Melanoplus flavidus</i> (Scud.)	*	*	*	—	—	—	—	—
<i>Melanoplus angustipennis</i> (Dodge)	*	*	*	—	—	—	—	—
<i>Melanoplus m. mexicanus</i> (Saussure)	*	*	*	—	—	—	—	—
<i>Melanoplus keeleri luridus</i> (Dodge)	—	—	—	*	*	—	—	—
<i>Melanoplus fasciatus</i> (F. Walker)	—	—	—	*	*	—	—	—
<i>Melanoplus gracilis</i> (Brunner)	—	—	—	—	*	—	—	—
<i>Melanoplus viridipes</i> (Scud.)	—	—	—	—	*	—	*	—
<i>Melanoplus walshii</i> (Scud.)	—	—	—	*	*	*	*	—
<i>Melanoplus punctulatus</i> (Scud.)	—	—	—	—	*	*	*	—
<i>Melanoplus scudderii</i> (Uhler)	—	—	—	*	*	—	—	—
<i>Shistocerca alutacea</i> (Harris)	—	—	*	—	—	—	—	—
<i>Phoetaliotes nebrascensis</i> (Thomas)	—	—	—	—	—	—	—	—
<i>Hesperotettix viridis pratensis</i> (Scud.)	—	—	*	—	—	—	—	—
Tettigoniidae								
<i>Scudderella furcata</i> (Brunner)	—	—	—	*	*	*	*	—
<i>Scudderella curvicauda</i> (DeGeer)	—	—	—	*	*	—	—	—
<i>Amblycorypha rotundifolia</i> (Scud.)	—	—	—	*	*	*	*	—
<i>Amblycorypha oblongifolia</i> (DeGeer)	—	—	—	—	*	*	*	—
<i>Pterophylla camellifolia</i> (Fabr.)	—	—	—	* ²	*	*	*	*
<i>Atlantius testaceus</i> (Scud.)	—	—	—	—	*	—	—	—
<i>Orchelimum sylvaticum</i> (McNeill)	—	—	—	—	—	—	*	—
<i>Conocephalus saltans</i> (Scud.)	—	—	*	—	—	—	—	—
<i>Conocephalus nemoralis</i> (Scud.)	—	—	—	—	—	—	*	—
<i>Ceuthophilus</i> sp. nymphs	—	—	—	*	?	?	?	?
<i>Ceuthophilus brevipes</i> (Scud.)	—	—	—	—	*	*	*	*
<i>Ceuthophilus maculatus</i> (Harris)	—	—	—	—	*	*	*	*
<i>Ceuthophilus latens</i> (Scud.)	—	—	—	—	*	*	*	*
<i>Ceuthophilus divergens</i> (Scud.)	—	—	—	—	—	*	*	*
Gryllidae								
<i>Gryllus assimilis</i> (Fabr.)	—	—	*	*	*	*	*	—
<i>Nemobius fasciatus</i> (DeGeer)	—	—	*	*	*	*	*	—
<i>Nemobius maculatus</i> (Blatchley)	—	—	—	*	*	*	*	—
<i>Nemobius carolinus</i> (Scud.)	—	—	—	*	*	*	*	—
<i>Nemobius confusus</i> (Blatchley)	—	—	—	—	—	*	*	—
<i>Oecanthus angustipennis</i> (Fitch)	—	—	—	*	*	*	—	—

* Report of A. E. Emerson.

Chicago. It reaches its eastern limits of distribution in northwestern Indiana. *Melanoplus flavidus* Scud., *M. angustipennis* Dodge and *M. mexicanus* Sauss. are also of regular occurrence on the foredune. Northwestern Indiana marks the eastern limits of distribution of the first two of these.

While not so abundant as in later stages of the succession *Spharagemon collare* Scud. may be considered characteristic of the foredune. *Diapheromera femorata* Say has been taken occasionally on the sand cherry. In these instances the growths of *Prunus* were near stands of oak (Dune Park, Ind.). These few records do not suffice to establish it as a regular inhabitant of the foredune associates but serve to exemplify the pitfalls of ecological studies based on general collecting of animals with which one is unfamiliar.

3. *The Poplar or Cottonwood Associates.* The most conspicuous and the dominant plants of this community are the species of *Populus*, chiefly *deltoidea* Marsh. Of significance to the Orthoptera are *Ammophila* and *Calamovilfa*, which persist from the earlier stage.

No species of Orthoptera are peculiar to the poplar associates nor is it characterized by the absence of any of the species occurring on the foredune. *Trimerotropis m. interior* is present in smaller numbers than on the foredune. The other foredune species are all to be found here. *S. collare* and *P. fenestralis* are somewhat commoner than in the preceding associates.

4. *The Pine Associates* is dominated by *Pinus banksiana* Lamb. This community develops only in sites protected from strong winds by dunes and is usually at some distance from the lake. The intensity of the physical factors operative is thus not altogether a direct result of modification by vegetation.

Conspicuous among the plants of the floor is the bearberry, *Arctostaphylos uva-ursi* Spreng., which forms considerable mats. The grass, *Andropogon scoparius* Michx., grows in scattered but numerous tufts in the unshaded parts of the community. Several species of *Vitis* are abundant.

As in the case of the poplar associates the pine community has no species of Orthoptera characteristic of it alone unless we so regard the three species *Hesperotettix viridis pratensis* Scud., *Photuliotus nebrascensis* Thomas and *Conocephalus saltans* Scud., which, however, are more typical of sand prairie and have been taken from among growths of pine at only one locality. They were found in the bunches of *Andropogon* and in the mats of *Arctostaphylos*. Of the Orthoptera found in the earlier associates all persist in the pine except *T. m. interior*. *M. angustipennis* apparently reaches its height of abundance in this stage of the succession.

Several species characteristic of the next successional stage are to be found at times in the pine community. *Arphia sulphurea* Fabr. is present in the adult stage until late May. *Gryllus assimilis* Fabr., *Nemobius fasciatus* DeGeer and *Tettigidea lateralis parvipennis* Harris, while not found during the summer, appear to invade the pine associates in September. *Parcoblatta pennsylvanica* DeGeer evidently moves into the pine associates nightly. Great numbers of unhatched and shriveled oothecae of this cockroach have been found

under the bark of pine logs. Hibernating nymphs of this species are also to be found in the pine community in October and November.

5. *The Black Oak Associes.* As the name indicates, the dominant plant of this community is *Quercus velutina* Lam. There is a fairly evenly distributed and abundant undergrowth composed of many species of shrubs, common among which are *Ceanothus*, *Gaylussacia*, *Vaccinium* and *Vitis*. Where the shade is not too heavy several grasses and sedges, *Panicum*, *Stipa*, *Aristida* and *Carex* grow on the forest floor.

The transition from pine to oak forest marks a rather abrupt change in the characteristic Orthoptera. While, as noted above, several species range from the oak into the pine associes these are by no means of universal or constant occurrence in the latter. Whereas the four earlier associes have several species in common, some of which range from pine to foredune, the oak forest possesses a distinctive fauna of Orthoptera. Apparently first in the colonization of the oak forest are *A. sulphurea* Fabr., *Spharagemon bolli* Scud., *Shistocerca alutacea* Harris and *Melanoplus keeleri luridus* Dodge. *M. fasciatus* Walker, *M. walshii* Scud. and *Chlocaltis conspersa* Harris are of discontinuous distribution in the black oak forest. *M. dawsoni* Scud. has been found in numbers in the scrubby growths of oak on the western shore of the lake. It reaches its southern limit of distribution in this longitude at Waukegan, Illinois, about thirty miles north of Chicago. Four species of Tettigoniidae and five of Gryllidae occur regularly in the black oak forest. There are two species of phasmids and two cockroaches. Table I indicates the species of Orthoptera found in the black oak forest on sand.

6. *The Red Oak-White Oak Associes* is not markedly different from the preceding in the herbaceous flora of the floor; such plants as *Panicum*, *Carex* and *Ceanothus* are found in both types of forest. Neither does there appear to be any conspicuous difference in the species of Orthoptera found in all the oak associes as they occur upon sand.

A similar forest is developed upon the clay west of the city of Chicago. A study of the Orthoptera in such a forest at Palos Park, Illinois, reveals that all the species characteristic of the oak forest on sand are present with the exception of *S. alutacea*. *M. keeleri luridus*, *S. bolli* and *A. sulphurea* are typical of the mixed oak-hickory forest on clay, being most abundant in the peripheral parts of the forest. To these are added *Atlanticus testaceus* Scud. and *Melanoplus viridipes* Scud. It is impossible to separate clearly the black oak from the red oak-white oak-hickory associes on the basis of the Orthoptera found in them. All the species listed (table I) are not to be found at any one locality but the association of certain species is not constant enough to enable recognition of definite successional stages indicated by the dominant trees. The one exception to this is the case of small, rather isolated tracts of black oak such as may be seen at Ogden Dunes, Ind. Here one encounters only the fully winged species which occur in the oak forests. This may be dependent merely upon the ability of these species to reach such isolated habi-

tats while the dissemination of the wingless types must be, of necessity, slower and through more continuous habitats. The increase in number of species in the oak-hickory forest on clay as compared with the oak forest on sand is probably, as will be pointed out, not due to differences in vegetation.

7. *The Subclimax Community* is not well exemplified in the Chicago region unless we accept the oak-hickory forest on clay as representative of this stage. A good development of this phase of the forest succession as it occurs upon sand is to be seen at Lakeside, Michigan. The transition from oak to subclimax forest is indicated by the establishment of such trees as *Acer*, *Fagus* and *Tilia*, and by the decrease in the amount of herbaceous vegetation.

The subclimax on sand at Lakeside has not been well studied due to its distance from Chicago. A few species of Orthoptera have been taken here, *Parcoblatta pennsylvanica* DeGeer, *P. virginica* Brunner, *P. uhleriana* Sauss., *M. viridipes* Scud. and *Ceuthophilus divergens* (Scud.). This stage of the forest succession is not included in table I because of the paucity of data concerning it. It appears, however, that the Orthoptera represented in this associes are also characteristic of both earlier and later stages.

8. *The Climax Forest* eastward from Chicago is dominated by *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. On the eastern shore of Lake Michigan at Saugatuck the hemlock forms a prominent part of the climax forest. West of Chicago the beech and hemlock do not occur and as a result the climax forest is an almost pure stand of sugar maple.

As regards both the herbaceous flora and the Orthoptera, the climax forest must be considered in two aspects. Where open spaces occur due to road-making or selective lumbering as at Smith, Indiana, and in the Pilcher Arboretum at Joliet, Illinois, considerable areas of the forest floor are covered by species of *Carex* and *Hystrix patula* Moench. Jewelweed, *Impatiens*, is a common herb of the climax forest. In the marginal parts and open spaces of the climax one encounters some of the species of Orthoptera typical of the earlier associes. At Smith, Indiana, along the edges of a small road through the forest, are found *M. walshii*, *C. conspersa*, *A. testaceus* and other species which occur in the oak and oak-hickory forest. These are more restricted in their distribution through the climax forest and distinctly fewer in number than in the oak or oak-hickory associes. A few specimens of *Melanoplus punctulatus* Scud. have been taken in the climax forests at Joliet and at Smith. The elongate or caudate phase of *T. lateralis parvipennis*, which is present in the oak associes, is represented in the climax by the abbreviate phase only, in which the pronotum reaches only to the tip of the abdomen.

The heavily shaded portions of the climax associes harbor only such secretive Orthoptera as *Nemobius confusus* Blatch. and a few species of *Ceuthophilus*.

The beech-maple forest at Lakeside, Michigan, represents a climax little affected by man. The leaf canopy is almost unbroken. The herbaceous flora

is limited to very few species but there is an abundant growth of the bed-straw, *Galium*.

Four species of *Ceuthophilus*, one cockroach and the katydid *Pterophylla* are known to inhabit this forest. No other Orthoptera have been taken or observed on several trips to this woods.

The distribution of the species of Orthoptera through the plant succession in the Chicago area is presented in condensed form in table I. This is not, of course, a complete species list for the region around Chicago but represents only those species encountered in the plant succession dealt with. It leaves out of account the Orthoptera found in such habitats as sphagnum bogs, prairie and stream margins.

PHYSICAL FACTORS

Quantitative determinations of various physical factors in the different stages of the forest succession have been reported by several workers from time to time. In spite of the fact that these measurements have been in most instances the summation of two or three years observations they are, as regards their usefulness in the present study, incomplete in some important respects.

1. *Evaporation*. This factor has been studied by Fuller ('12) and his students. A resumé was published by this author in 1914. He found a high rate of evaporation in the poplar associates during the summer, amounting to an average of twenty-two cc. per day. While he has published no data on this factor in the foredune associates it is probable that a similar condition prevails there. Evaporation in the pine associates is about half that in the poplar and about equal to that in the black oak community. It diminishes successively but not greatly in the other associates.

This work was done from the viewpoint of the botanist; the determinations of evaporation were made at a height of 20–25 cm. above the earth. This does not indicate exactly the conditions to which a ground-frequenting insect would be subjected. It is, however, only in the case of the pine associates that the data given seem insufficient for the purpose of the present article.

The pine community is one where stress of physical factors is sharply delimited. Fuller's measurements were made in sites shaded through the greater part of the day. Fully three-fourths of the area of the complex called pine associates is subjected to full solar radiation through much of the day. Hence the data of Fuller do not answer the question of evaporation rates in exposed sites in the pine community and especially that prevailing on clear summer days when surface temperatures are very high. No further data, however, are available. Figure 1 shows the progressive decrease in the evaporating power of the air through the plant succession, with conditions in the poplar community taken as unity (22 cc. per day).

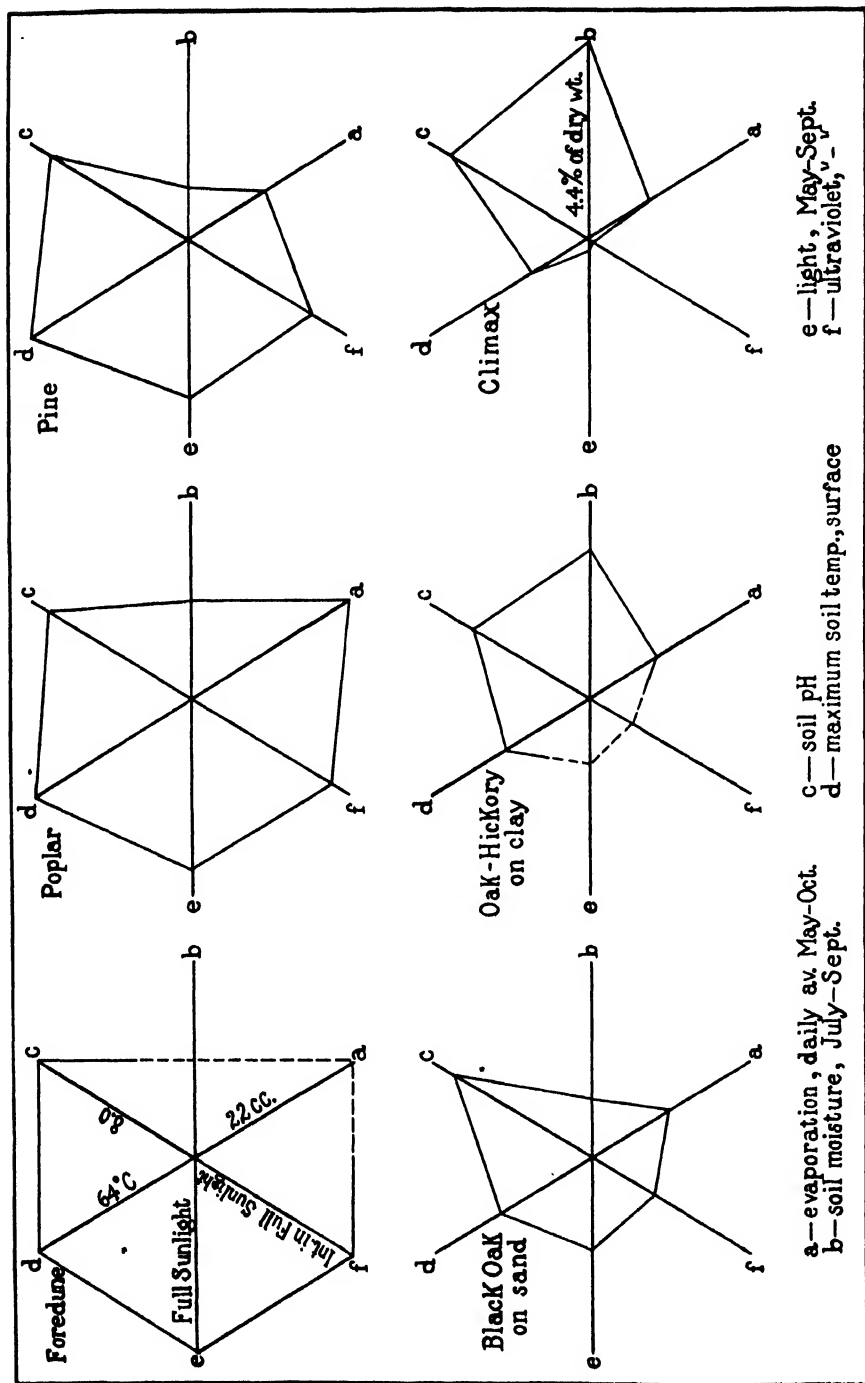


FIG. 1. Physical factors in the plant associates described. In the case of sunlight the average daily total during the period May-September 1935 was 430 G.-cal./cm.²/min. (Pyreheliometer records of meteorological station. University of Chicago.)

2. *Soil Moisture.* Fuller ('12a, '14) found the amount of growth-water to be greatest in the beech-maple forest (4.4% of dry wt.) during the summer and early autumn. This condition is taken as unity. Growth-water (that available to plants) probably represents, in general, the amount of water available to all organisms. Fuller found that a dry mulch of sand three to five cm. thick preserved the deeper water in the cottonwood associates and, due to its sparser vegetation, the amount of ground water here was greater than in the pine and black oak associates.

3. *Soil pH.* Kurz ('23) published the results of determinations of this factor. The great variation of soil pH in sites close together precludes any conclusion as to the average of this condition. This variability is most marked in the more advanced associates. Kurz reports a pH of 4.5 where wood had decayed.

The points plotted on the pH axis in Figure 1 are representative soil pH measurements in the different associates. Only the top layers of soil are considered here. From Kurz's data and discussion it appears that in the sand dunes decreasing alkalinity is due for most part to the leaching out of basic material carried in the wind-blown sand. Leaching seems to be the most important factor in the change in pH of moraine soils as the flood plains in such areas are consistently more alkaline than the hills.

The pH axis is, of course, a logarithmic device. Hence the length of these axes in the figures for the different associates is not in proportion to that of the other axes. The greatest alkalinity is found in the sand of the fore-dune (pH 8.0). This is gradually reduced to neutrality (pH 7.0) or, in some sites in the pine associates, to slight acidity (pH 6.0). From Kurz's data it appears that neutrality is the most common condition of the soils of the pine, oak and climax associates on sand while the soil of the forests on clay is neutral or slightly acid (pH 6.0).

4. *Soil Temperatures.* Determinations of this factor in the course of the present study have demonstrated high extremes of surface temperatures (64° C.) in the fore-dune, poplar and pine associates on clear summer days. It appears that moderate soil temperatures are never surpassed in the oak forest; the maximum measured was 38° C. In the most perfect development of the climax forest, which was studied as found at Lakeside, Michigan, the highest surface temperature recorded was 24° C. In the spring the exposed areas of sand in the fore-dune, poplar and pine associates respond quickly to increased air temperatures and greater intensities of solar radiation. Soil temperatures in the oak and climax forests lag considerably. This lag is particularly marked in the latter community. In 1935 soil temperatures of 20° C. or above were not reached in the climax forest until July according to the records taken.

The annual minimum soil temperatures at a depth of two inches are very nearly the same for all the associates. The lowest recorded was —3.5° C. in the poplar community. The difference between this and the simultaneous

record for the climax, — 1.5° C., is hardly of significance in the survival of the eggs of Orthoptera which occur in this latitude.

Thermograph records for August and September indicate that average soil surface temperatures in the oak forest and in well shaded sites in the poplar and pine associates are approximately equal to average air temperatures. Average temperatures at a soil depth of two to six inches are one to two degrees lower than at the surface during August and September. Surface temperatures in the climax forest average from one to five degrees lower than air temperatures for this period. The greatest deviation is on days of fairly high air temperatures and is probably greater in the early summer.

The maximum soil surface temperatures recorded in the different associates are shown in figure 1.

5. *Sunlight Intensities* were measured by O. Park ('31) by means of the McBeth illuminometer. By determination of the relative areas in full sunlight, in sunflecks and in shade, and by measurements of light intensities in each of such sites he has reduced sunlight intensities in the various associates to a standard designated by him the Ecological Light Unit. The basis of comparison is the intensity of full sunlight; light intensities in the plant communities are expressed as a per cent of full sunlight. Thus the poplar and pine communities receive about 80–90 per cent as much solar radiation at the earth's surface as do such open sites as the foredune. A marked diminution in this factor occurs in the transition from pine to oak forest; sunlight intensity on the floor of the latter associates is approximately half that in the former. Solar radiation falling on the floor of the climax forest amounts to only 5 per cent of that incident upon the foredune. The foregoing description applies, of course, only to the season extending from about May 1 to October 1.

Maximum soil temperatures show, as would be expected, a direct and rather close correlation with intensities of solar radiation.

The oak-hickory forest on clay was not considered separately by Park. The point on the sunlight axis for this associate is an approximation arrived at by a consideration of the general aspect of the sunfleck pattern of the floor as compared with those of the black oak and climax forests.

6. *Ultraviolet Radiation* was measured by photochemical and photoelectric methods in the present investigation. When the data were reduced to a standard similar to the Ecological Light Unit of Park it was found that in the case of total ultraviolet (2900–3900 Å) the diminution in intensity through the forest series is similar to that of visible light although more decided. The intensity of this radiation in the climax forest is less than one per cent that in full sunlight.

Ultraviolet of wave-length 3100 Å and shorter is apparently absent in the oak and climax forests except in sunflecks and clearings. While this spectral fraction is not indicated in figure 1 its successive diminution resembles that of total ultraviolet.

DISCUSSION

The succession of one plant associates by another effects, of course, a change in a complex of physical factors. It is entirely possible that two or even more of these are concerned in an inseparable manner in determining the local distribution of Orthoptera. There are in some instances, however, marked changes in only one factor, which, therefore, appears to be the decisive influence in the occurrence of certain species.

An inspection of table I shows that of the seven species of Orthoptera which are found on the foredune six range through the poplar and into the pine associates, while one extends only into the poplar community. The general aspect of this group of Orthoptera is distinctly western. *T. maritima interior*, however is an inland race of a species which occurs along the Atlantic coast from southern Maine to Florida. *Interior* ranges along the southern shores of the Great Lakes and along streams into Iowa and Minnesota. Both it and the typical form are confined to sandy areas near water. The other six species of the foredune have wide western ranges. Northwestern Indiana marks the eastern limits of *A. deorum*, *M. angustipennis* and *M. flavidus*. The first two of these range southwestward into Arizona and northwestward to British Columbia. *M. flavidus* reaches southern Colorado. Blatchley ('20, p. 417) says that it is known from Tucson, Arizona.

S. collaris, *P. fenestralis* and *M. mexicanus* range extensively east, west and south of northern Illinois. *M. mexicanus* is reported as much more abundant in the western part of its area of distribution.

Reference to figure 1 will show that the foredune and poplar associates are much alike in their physical factors. There is only a slight modification of light and ultraviolet intensities. The soil pH in the poplar associates approaches neutrality from the slightly alkaline condition of the foredune. No actual measurements of evaporation and soil moisture on the foredune have been made but these factors are certainly not less than in the poplar associates. From Fuller's discussion of the effect of vegetation on soil moisture one would expect more available water on the foredune than in the poplar community. With this similarity of environment we find (table I) seven species of Orthoptera common to the two associates and none peculiar to either.

The transition from poplar to pine associates is marked by a decrease in soil moisture; soil water in the pine community amounts to only half that in the poplar dune, probably, to the demands of the abundant vegetation. There is a decided decrease in the rate of evaporation as determined by Fuller. The vegetation of the pine dune is quite different from that of the first two associates discussed. This difference, in Fuller's opinion, is best correlated with diminished evaporation. The other physical factors undergo little modification in the transition from poplar to pine community.

Of the species of Orthoptera present in the first two communities one only, *T. maritima interior*, is absent from the pine dune. Its local distribu-

tion appears best correlated with soil water. Its geographical range also suggests a dependence upon the amount of soil moisture as it is restricted to sand areas near water east of the ninety-fifth meridian. The other species, with the exceptions of *S. collare* and *M. mexicanus*, are, in the Chicago area at least, peculiar to sand. Their limitation to this type of soil is probably a phenomenon depending upon the more constant and always moderate supply of soil water in sand as contrasted to clay soils (Fuller, '14, p. 227). The exclusion of *interior* from the pine dune community would be interpreted, according to this hypothesis, as due to a greater minimum requirement in this respect than is the case with the other species. If we assume the validity of this suggestion the critical point would be the selection of sites for oviposition or the early development of the eggs or both, since it is only in the summer and early autumn that soil water is deficient in the pine associates.

M. mexicanus is an abundant species on the high prairie of the moraine region *S. collare* has also been found on clay hills where there is some sand mixed with the glacial till, as along the fossil shoreline near Smith, Indiana. Unshaded and well drained clay soil in this region is characterized by great extremes of soil water; the moisture content is very high during winter and spring while pronounced desiccation takes place in the summer. The tolerance of these two species for both extremes of soil moisture locally is also suggested by their extensive distribution. Both range from the Atlantic states to Utah and Arizona.

The succession of the pines by the black oaks brings about little change in soil moisture, soil pH and evaporation (fig. 1). The most radical changes in the physical factors occur in the cases of light, ultraviolet and maximum soil temperatures.

From table I it is apparent that the transition from pine to oak forest marks an important zone of tension in the succession of Orthoptera. Of the twenty-three species listed from the black oak forest only five occur in the pine associates and these are of sporadic appearance. On the other hand, of the thirty-one species found in the oak-hickory forest on clay, which differs markedly from the black oak forest on sand only in the matter of soil water, twenty-two or 71 per cent are also to be found in the black oak forest on sand.

The change in the characteristic species of Orthoptera in the transition from pine to black oak forest is best correlated with sunlight intensities and soil temperatures. The correlation with ultraviolet intensities is, judged from experiments made in the course of this study, superficial only. No basic importance to Orthoptera of this radiation has been demonstrated. The correlation with light intensities is very likely not due to its visual effect. Observations in the forest show a concentration of nymphs of Orthoptera around the margins of clearings and in sunflecks, especially in May. This fact was noted by Shelford ('13, p. 241). It has been observed that nymphs of *A. testaceus* and *M. viridipes* which were in a clearing exposed to full

solar radiation retired to shaded sites when soil surface temperatures rose to 35° C. The nymphs of *A. testaceus* often crawled beneath the mat of leaves on the ground. Since this behavior took place about an hour later than the incidence of daily maximum sunlight intensities (11:45 C.S.T.) it appears to have been a reaction to heat rather than to light as illumination. The increased rate of evaporation with higher soil temperatures has not been determined; possibly this factor exercises an important influence in the behavior described. Again, there is a migration of *A. sulphurea* from the pine into the oak forest in late May. From Fuller's data ('14, p. 201, 202) it appears that the rate of evaporation in the two associates is not greatly different at this time. His determinations, however, were not extended to the more open parts of the pine community. Since soil surface temperatures in such exposed sites are known to surpass 50° C. in late May, evaporation in the air immediately above the sand must be greatly increased. This condition prevails over three-fourths or more of the pine associates; areas of moderate soil surface temperatures are limited to small, heavily shaded spots almost or quite devoid of herbaceous vegetation and unsuited to the existence of Orthoptera.

The suggestion that sunlight is not of greatest importance because of its visual effect is substantiated by the experiments of Langford ('30), who found no difference in the growth rate of nymphs of *M. bivittatus* in darkness and in light when temperatures were maintained at a predetermined optimum. Since the species used lives naturally in environments where it is exposed to high intensities of sunlight this experiment must be considered as having definite bearing on the rôle of sunlight in the ecology of Orthoptera. Temperature was not adequately considered in the experiments of Nabours, Larson and Hartwig ('33) and of Sabrosky, Larson and Nabours ('33), who reported a positive effect of light on the growth of grasshoppers.

The abrupt dropping out of the species found in the preceding associates is also best correlated with diminished sunlight intensities and lower soil temperatures. Soil temperatures in the oak forest lag behind those of open sites in the annual rise in April and May. It is entirely possible that the higher soil temperatures prevailing at this season in the earlier associates may be essential to the development of the Orthoptera which are confined to these communities. The direct utilization of radiant energy as heat by the growing nymphs may also be of significance. Such an assumption seems to explain best the results of the experiments of Sabrosky, Larson and Nabours which have been cited.

Graham ('20) has showed that the temperature of logs exposed to direct sunlight may rise above 50° C. on summer days. Such temperatures would act upon the eggs of such species as *Chloealtis conspersa*, *M. walshii* and the species of *Parcoblatta*, which use logs as sites of oviposition. That such is the case is indicated by the finding of numbers of unhatched and shriveled oothecae of *P. pennsylvanica* under the bark of pine logs. Graham consid-

ered the high temperatures of such habitats the most important factor in conditioning the fauna.

The oak-hickory forest on clay as exemplified at Palos Park, Illinois, is not greatly dissimilar to the oak forests on sand in respect to its fauna of Orthoptera. As pointed out before, these two associates have twenty species in common with one species confined to the oak forest on sand while ten species which occur in the oak forest on clay have not been taken in the similar forest on sand. In the case of such nocturnal species as *A. oblongifolia* this may be the result of oversight as night collecting has not been done in the dunes and these insects, where they occur, are not much in evidence during the day. The use of molasses traps for *Ceuthophilus* in the dunes has been wholly unproductive. A few nymphs of some species of this genus were found in a black oak forest on sand at Saugatuck, Michigan.

The only marked change in the physical factors from the black oak to the oak-hickory forest (fig. 1) is in the matter of soil moisture. Hence this is suggested as the factor the increase of which allows the advent of such Orthoptera as *Ceuthophilus*, *M. viridipes*, *M. gracilis* and *A. testaceus*. That the occurrence of these is not due to the fundamental properties of clay is shown by their establishment in the climax forest on sand at Saugatuck, Michigan, and, in the case of *M. viridipes*, its presence in the subclimax on sand at Lakeside, Michigan.

Where clearings are present in the climax forest several species of Orthoptera which also occur in the preceding associates have been taken. To these are added four species which, insofar as the series of habitats under discussion is concerned, are characteristic of the climax forest only. The beech-maple forest at Lakeside, Michigan, presents an almost unbroken leaf canopy, very low sunlight intensities in summer and low maximum soil temperatures. Here the number of species of Orthoptera is greatly reduced. Four species of *Ceuthophilus* have been found under logs and the katydid *Pterophylla* has been heard in the trees.

The low sunlight intensities and low soil temperatures in this type of habitat appear to be decisive factors in the limitation of the fauna of Orthoptera. Evaporation is 25 per cent less than in the oak-hickory forest and averages only 7 cc. per day during the summer. While Hamilton ('36) has demonstrated that too great humidity is detrimental to some locusts one can make no suggestion as to the effect of atmospheric moisture in the climax forest. Parker ('30) gives 17° C. as the temperature threshold of *M. mexicanus* eggs. Such soil temperatures have not been recorded in the climax forest until late June and July in the measurements made in the course of this study, which suggests that this factor is an important one in the exclusion of many species of Orthoptera. On the other hand the restriction of the low vegetation of the forest floor to *Galium* could well be the decisive influence.

Little attention has been directed to soil pH in the foregoing discussion. While the author is not aware of any experimental work on the effect of this

factor on the eggs of Orthoptera, investigation of the effect of relatively narrow ranges of pH on animals has produced, in general, negative results. Even in the case of such organisms as earthworms, which live in very intimate association with the soil, Allee, Torvik *et al.* ('30) conclude that a range of pH 6.0–8.0, which is that dealt with at present, is not of direct significance in influencing distribution.

Considerable attention has been directed by field orthopterists to the vegetation with which certain species are often associated. While it is possible to define a very good correlation in a limited area, experimental evidence indicates a very wide latitude in the food requirements of all the species which have been reared under laboratory conditions. There are, undoubtedly, some plants upon which Orthoptera will not thrive (Carothers, '23) but such plants as can be used as food for one species are equally useful for others. As Morse ('99, p. 315) says, their food requirements are "... general in character rather than special, a question of quantity rather than quality." In this laboratory *M. differentialis*, *M. viridipes*, *A. sulphurea* and *A. testaceus* have been reared on lettuce and alfalfa hay, *Poa* and various other grasses. Adults of *T. maritima interior* and *M. fasciatus* have fed freely on maize leaves, lettuce and wheat sprouts and have mated and oviposited while on this diet. *M. punctulatus* nymphs taken from beech and maple trees were reared to maturity on the leaves of elm. This species has been observed feeding on the tamarack and cassandra (*Chamaedaphne*). In the light of such evidence it does not seem probable that the occurrence of certain Orthoptera is strictly dependent upon particular plants. Moreover the distribution of some species of Orthoptera is much more restricted than that of the plants with which they are often found. The converse of this is equally and, in the case of destructive species, forcibly true.

There appears to be no lack as to the quantity of plant material available for food in any of the communities described unless it be in the climax forest. The most primitive community, the beach, is practically bare of plants. While no actual data have been taken on the relative quantities of herbaceous vegetation the rather abundant growths of grasses in the earlier associates are not perceptibly affected by the feeding of the grasshoppers found there.

It seems, from the results of this study, that the controlling factors in the local distribution of the Orthoptera of the Chicago area are sunlight, as heat, and soil moisture. This conclusion is similar to that arrived at by Dreyer and T. Park ('32) in a study of the factors determining the situation of the nests of *Formica ulkei* Emery. Talbot ('34, p. 419) cites instances of the effect of soil temperature on the behavior of ants. Chapman, Mickel and Parker ('26) found that confinement to sand at 55° C. for one minute was sufficient to kill *Gryllus assimilis*. *Spharagemon aequale* (*collare*, Hebard, '32, p. 30) was able to survive for much longer periods, even with its wings clipped, by extending its legs and thus raising its body from the hot sand. They also found, in laboratory experiments, that the crickets died at a tem-

perature of 49° C. with paralysis beginning at 42° C. The grasshopper *Spharagemon*, which inhabits open situations in the dunes, died at 55° C. with paralysis beginning at 50° C.

It is improbable that evaporation has no effect in the distribution of Orthoptera. The only experiments relating to this factor have been performed using relative humidity as the index to moisture conditions in the atmosphere. Hamilton ('36), using two species of African locusts, found rather wide latitudes of this factor tolerated. At temperatures of 80–90° F. *Locusta migratoria* developed at R.H. 35–85 per cent. *Shistocerca gregaria* was less tolerant in this respect, developing only at R.H. 45–75 per cent. The absence of absolute meaning in relative humidity makes impossible any close comparison of experiments using this factor with natural conditions studied by means of evaporimeters.

A comparison of Talbot's ('34) experiments on ants with those of Chapman, Mickel and Parker ('26) on insects of various orders suggests high soil temperatures as a more effective and more rapidly acting lethal factor than is evaporation as indicated by relative humidity. Whereas in Talbot's experiments ($T = 41^{\circ}\text{C.}$; R.H. = 8%) individuals of the least resistant ant species survived for fifty minutes, in the experience of the latter workers a few minutes at 50–55° C. were sufficient to kill those insects not adapted in some manner to the high surface temperatures of sand. Mosauer ('36) found that desert reptiles died within nine minutes when confined to sand at a temperature of 55–60° C. The critical body temperature was between 40° and 45° C. While these last experiments used animals entirely different from those under consideration they serve to illustrate the effectiveness and rapidity of action of high soil temperatures in restricting the range or, in some instances, the time of activity of animals. In the case of insects evaporation produced by these high temperatures must play some part. One could demonstrate, probably, a differential susceptibility to this factor in species of Orthoptera from different habitats as did Talbot with ants.

The restriction of certain species of Orthoptera to sand in this area appears to be a phenomenon dependent upon the fairly constant supply of water in this type of soil and the absence of either extreme of soil moisture. Fuller ('14) has demonstrated the difference in this respect between sand and clay soil in the region about Chicago. In the entire complex of Orthoptera found in this area no species is restricted to clay soil while thirteen species are confined, apparently, to sandy soil. Since the same or closely related species of plants are to be found on both types of soil and other factors such as sunlight and evaporation are similar in habitats of equal exposure, soil moisture seems clearly to be the controlling influence in determining the orthopteran fauna of sand as contrasted to clay.

There appear to be very local influences, particularly in the oak-hickory forest on clay, which effect a differential distribution of the species within the area covered by one associates. The topography of the land suggests soil

water as affected by drainage as the main factor operative. Thus in the forest of this type most studied *M. viridipes* and *A. testaceus* are most abundant on the sides of a broad, gently sloping ravine while *M. fasciatus* and *M. keeleri luridus* are almost wholly restricted to the high parts of the forest. If we assume, as is likely, that the soil of the ravine has a greater moisture content than has that of the more elevated portion of the forest the very local distribution of these species corresponds to their occurrence in the associates considered. The first two are absent from the oak forest on sand, where soil moisture is small in amount, while the latter two are to be found in such habitats. *Luridus* especially is characteristic of the oak forest on sand. That their local distribution depends in large measure on differences in soil moisture is substantiated by their geographic ranges; the Mississippi River marks the approximate western extension of *M. viridipes* and *A. testaceus*; *M. fasciatus* and *M. luridus* range westward to and beyond the one hundredth meridian.

Morse ('04) offered a classification of locust societies based upon a primary division into geophilous and phytophilous groups. Each of these he further separated into campestrian and sylvan assemblages of species. The designations of these and of the lesser groupings suggested, saxicolous, arenicolous, humicolous, are descriptive of the gross features of the habitats. While in a general descriptive way Morse's classification is entirely valid my own experience is in accord with that of Shull ('11), who noted that conditions of a very local nature were often of great importance, a fact not overlooked, however, by Morse.

TABLE II. Schematization of the communities of Orthoptera as suggested by their distribution in the Chicago area compared to the arrangement of the plant communities as recognized by botanists

Orthopteran community	Plant community ³
(A) <i>Spharagemon collare</i>	Foredune, Poplar, Pine
(1) <i>S. collare</i> - <i>T. m. interior</i>	Foredune, Poplar
(2) <i>S. collare</i> - <i>M. angustipennis</i>	Pine
(B) <i>Parcoblatta pennsylvanica</i>	Black oak, Oak-hickory, Subclimax on sand, Climax
(1) <i>P. pennsylv.</i> - <i>M. k. luridus</i>	Black oak, Oak-hickory in part
(2) <i>P. pennsylv.</i> - <i>M. viridipes</i>	Oak-hickory, Subclimax on sand, Climax in part
(3) <i>P. pennsylv.</i> - <i>Ceuthophilus</i>	Oak-hickory in part, Subclimax on sand, Climax

³ Cowles, '01.

It is evident (table I) that the ecological distribution of Orthoptera in the Chicago region is not indicated in an absolute manner by the dominant plants of the associates considered. When these insects alone are considered they appear to be grouped into two major assemblages of species, which we may designate the *Spharagemon collare* and the *Parcoblatta pennsylvanica* com-

munities. The first of these corresponds to the foredune, poplar and pine associates of plant ecologists, the second to the black oak, oak-hickory, subclimax on sand and climax associates. Solar radiation intensities seemingly serve as the best indices of these primary divisions.

There are two aspects of the *S. collare* assemblage, one of which is indicated by the presence of *T. maritima interior* but which also includes all the other species. This we may call the *collare-interior* community. The other, characterized by the great abundance of *M. angustipennis*, is aptly described as the *collare-angustipennis* community. The division in the major *collare* group is brought about by differences in soil water as judged by the data available.

The other primary assemblage of species occurs in three intergrading aspects. We may designate the secondary groups the *P. pennsylvanica*-*M. k luridus*, the *P. pennsylvanica*-*M. viridipes* and the *P. pennsylvanica*-*Ceuthophilus* communities. As is apparent in table II the groupings suggested here do not coincide with the associates as schematized by plant ecologists.

The delimitation of the first two of the secondary groups of the *P. pennsylvanica* assemblage (insofar as it exists) appears again to be an effect produced by differences in soil water. Suggestion as to the specific factor or factors operative in the segregation of the *M. viridipes* and *Ceuthophilus* communities is not so readily made although sunlight intensities and resultant temperatures are indicated.

SUMMARY

The physiographical and vegetational features of the plant succession on sand and of two types of forest on clay in the Chicago region are reviewed.

Quantitative determinations of the physical factors operative in these associates are also reviewed.

The species of Orthoptera characteristic of these associates are listed and discussed.

It is concluded that the change in the typical species of Orthoptera from foredune to pine associates is dependent upon decreasing soil moisture.

Sunlight intensity appears to be the principal factor operative in the faunal change from pine to black oak-associates. Its action is apparently as heat rather than as illumination.

The greatest number of species of Orthoptera is found in the oak-hickory forest on clay. This is correlated with an abundant soil moisture, a middle range of light intensities and moderate soil temperatures.

The greatly reduced number of Orthoptera in the climax forest may be due to low soil temperatures or to lack of variety of herbaceous vegetation.

The restriction of certain species to sand may be accounted for on the basis of a requirement of soil moisture of more constant amount and of lesser extremes than is the condition in clay soil.

Two major communities of Orthoptera are recognized among the species

dealt with. One of these is divided into two, the other into three lesser groups.

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THE INTERCEPTION OF PRECIPITATION IN AN OAK-PINE FOREST

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Many experiments have been conducted in various parts of the world to determine what portion of the precipitation falling on tree crowns eventually reaches the ground. Horton ('19), Zon ('27), and Burger ('33) have reviewed and summarized some of these earlier studies. More recently Beall ('34), Mitchell ('30), and Simson ('31) have studied the interception of precipitation at different localities and in different forest types. In the course of other studies, Maule ('34) made some observations of the interception of snowfall by both conifers and hardwoods, and Holch ('31) measured the interception of summer rainfall in an oak and in a linden forest. In most of these studies it has been shown that the amount of precipitation reaching the ground in the forest varies with the character of the forest, character of the precipitation, and the wind velocity, among other factors. Because of these variables it is evident that precipitation records made in one forest type and age class cannot be of general application.

In southern New Jersey a lack of seedling reproduction and the prevalence of fire are two of the principal forest problems. Both are made more difficult of solution by the partial interception of precipitation by the tree crowns. The Allegheny Forest Experiment Station has therefore made an effort to measure this interception.

In a forest typical of the northern edge of the New Jersey Pine Barrens, four standard U. S. Weather Bureau rain gauges (8-inch) were set up within an area of about $\frac{1}{20}$ acre on the Station's Camp Ockanickon Experimental Forest, southeast of Medford. One gauge was placed under a chestnut oak (*Quercus montana* Willd.), one under a pitch pine (*Pinus rigida* Mill.), a third under a white oak (*Q. alba* L.) which was partly overtopped by a pitch pine, and the fourth was placed under a small gum (*Nyssa sylvatica* Marshall) which was overtopped by a chestnut oak, the latter being in turn overtopped by a pitch pine. Although seven other species occurred in this particular stand, the four species mentioned above made up about 90 per cent of the total. The oaks and pines were about 90 years old and were from 40 to 60 feet high, whereas the gum, having come in to the stand at a much later date, was confined to the understory.

The four rain gauges in the woods, and a fifth gauge located in the open

* Maintained by the U. S. Department of Agriculture at Philadelphia, Pennsylvania, in cooperation with the University of Pennsylvania.

at a site 10 chains away, were read from May 6 to November 8, 1932. In 1933 a second gauge was established in a clearing about one mile from the other in the open. To determine if there was any local fluctuation in precipitation this gauge was read simultaneously with the other five from June 26, 1933, to May 29, 1934. During these two periods—one of approximately 6 months, the other of 11—measurements were made of the precipitation from 145 storms, ranging in amount from a trace to 3.89 inches. Eleven times during the period the precipitation fell as snow; at all other times, as rain.

Early in the study it was thought that successive readings made when the rain ceased, and at short intervals thereafter, would give some measure of the precipitation that finally dripped to the ground. It was found, however, that the amount of this afterdrip was negligible.

Table I shows the total precipitation caught in the five gauges during the periods named.

TABLE I. *Precipitation passing through tree crowns of various species compared with that falling in the open*

Gauge No.	Type of cover	Precipitation		Per cent of gauge 1
		Total inches	Mean per storm	
1	None	71.65	.494	100
2	Pine	60.81	.419	84.9
3	Oak	60.81	.419	84.9
4	Pine and oak	65.41	.451	91.3
5	Pine, oak, and gum	62.77	.433	87.6
Mean of gauges 2-5 inclusive		62.70		87.2

The readings for gauges 4 and 5, as revealed in this table, are somewhat unexpected; it might be assumed that a gauge overtopped by the crowns of two or by three trees would receive less water than the gauge which was overtopped by only one tree. They are not illogical, however, if the infinite number of branch and leaf arrangements possible in a tree crown, and the continuous changes taking place in them, are considered. Furthermore, as is shown below, the precipitation caught in a single 8-inch gauge under a tree may be an inadequate sample of the total which falls through the crown of that tree.

To test the significance of the data in table I, as well as to compare the readings of the two gauges in the open, one of which does not appear in the table, Fisher's analysis of variance method, as interpreted by Snedecor ('34) was used.¹ By this method the variation traceable to a specified source, such as variation in amount of precipitation as between storms, can be segregated.

The performances of the two gauges in the open were compared by using the data collected during a period in which precipitation fell 90 times. There

¹ Method suggested by G. Luther Schnur, Associate Silviculturist at this Station.

was no significant difference. In other words, for the period of the record, there was no real variation in the precipitation falling in the open within one mile of the five gauges first established.

Similar tests revealed a significant difference in performance between the one gauge in the open and each of the four gauges in the woods.

Whether or not these four gauges in the woods were sufficient to obtain an adequate sample of the precipitation penetrating the crowns of a forest of this character might be questioned. Consequently the readings from the four gauges in the woods were compared statistically. That these comparisons showed a difference that was significant, although only slightly so, indicated that too few gauges had been used in the woods. In order to determine how many gauges would be necessary in the woods to get as close a correlation as that obtained between the two gauges in the open, the familiar formula

$\sigma_m^2 = \frac{\sigma^2}{\sqrt{N}}$ was used. Substituting the standard error of the mean of the measurements taken from the two gauges in the open for σ_m and for σ the standard deviation of the measurements taken from the four gauges in the woods, then solving for N , the result is 18. Conceivably a number smaller than this would be adequate to eliminate all significant variation between the gauges in the woods even though the high degree of accord between the gauges in the open was not attained.

In spite of the apparent inadequacy of the sample obtained in the woods some of the results of this study are in accord with those obtained by other investigators. Mitchell ('30) and others have shown that the relative amount of precipitation which penetrates the crowns increases as the storm increases in magnitude and duration. In the present study it was found that this increase was most rapid as the precipitation increased up to 0.3 inch and when the amount reached 0.75-inch 91.3 per cent of it penetrated the crowns. For intensities above 0.75-inch the increase in penetration was slight.

The character of the precipitation as well as its magnitude and duration has been cited above as one of the variables affecting interception. As a check on this, the precipitation from the 11 snow storms, which occurred during the period of observation, was compared both in the woods and in the open with that from 11 selected summer rains of almost equal magnitude. Only 68.2 per cent as much of the snow water reached the ground in the woods as in the open, whereas 78.1 per cent as much of the rain fell in the woods as in the open.

Regardless of the character of the precipitation, some increase in the proportion penetrating the crowns might be expected under deciduous trees after the leaves fell. However, the contrary was true. From 56 winter storms, slightly less water reached the gauge under the chestnut oak than reached the same gauge from 56 summer storms of almost equal magnitude. This was true even when snow storms were eliminated from the calculations. Beall ('34) found that presence or absence of hardwood foliage had little influence

on the percentage of rainfall reaching the forest floor. Mitchell ('30) however, found that there was an 8.8 per cent increase in the precipitation which reached the ground in the fall after the leaves were down.

SUMMARY

Four raingauges set up in a mixed forest of oak, pine, and gum were read following 145 storms. The total precipitation caught in these gauges varied from 84.9 to 91.3 per cent of that caught in a gauge in the open nearby. The average catch for the four gauges in the woods was 87.2 per cent of that caught in the open.

A statistical analysis of the data showed that there was a significant difference between the readings made in the woods and those in the open. There was also a barely significant difference among the gauges in the woods, indicating that too few gauges had been used. Further computations showed that the number of gauges in the woods should have been increased to eighteen.

The proportion of the rain reaching the ground in the woods increased with the intensity and duration of the storm. For the average storm of 0.75 inch recorded in the open, 91.3 per cent reached the ground in the woods.

A smaller proportion of precipitation penetrated the crowns when it fell as snow than when it came down as rain.

The proportion of precipitation which penetrated the crown of a chestnut oak did not increase after the leaves fell.

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ACTIVITY AND HOME RANGE OF THE FIELD MOUSE,
MICROTUS PENNSYLVANICUS PENNSYLVANICUS
(ORD.)

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The present paper results from a projected study designed to analyze the dynamics of cyclic phenomena in mammals.

PERIOD OF ACTIVITY

Conflicting testimony regarding the activity of *Microtus* has been recorded by various writers. Grinnell ('08) indicates that the Californian voles (*Microtus californicus*) appear more active by daylight, when greater numbers are trapped. Hatt ('30) states that *Microtus*, though up and around at any hour of the day, is chiefly nocturnal, but he presents no evidence to substantiate this statement. The conclusions of Hatfield ('35), from observations on captive *Microtus californicus*, suggest relative quiet on the part of the mice during the day, the animals becoming more active at night. He adds that observations of others with the same species would indicate greater activity by these voles during the day than night. Hatfield suggests that the rhythm of activity in *Microtus* is modified by localized temperature conditions. Dice and Sherman ('22) state that *Microtus* is "more active in the evening just before sunset."

The most elaborate studies of microtine activity have been those of Davis ('33) who studied the British *Microtus agrestis*. Captive individuals were housed in cages so constructed that any movement of the animals would be relayed to a recording kymograph. His observations clearly demonstrate that this vole has a short 2 to 4 hour rhythm of feeding activity and a longer 24 hour rhythm with its peak following sunset and a higher average of activity at night. Voles kept in total darkness for 24 hours maintained both rhythms. These experiments suggest that *Microtus agrestis* is chiefly nocturnal. Similar short period activity of the albino rat has been correlated by Richter ('27) with a hunger response brought about by regular stomach contractions.

Although deer mice (*Peromyscus*) are largely nocturnal, it has been shown that these rodents exhibit rhythmic activity. Thus Johnson ('26) has shown that there is a well marked rhythm of activity which persists in the absence of any daily change of light, but the rhythm may be reversed or otherwise modified by the use of light. Johnson found the greatest activity of mice shortly after dark. Elton, Ford and Baker ('31), who studied the

long-tailed wood mouse (*Apodemus sylvaticus*), give some evidence to support the view that greatest activity occurs at dusk, shortly after midnight and again at dawn. *Apodemus* is strictly nocturnal. Lately Behney ('36) has confirmed the studies of Johnson ('26) but found captive *Peromyscus* were active in outdoor cages when these were covered with snow. In central New York the writer has seen indications of subnivean activity on the part of deer mice during daylight hours.

METHODS

While it is considerably more difficult to secure data on this subject from field investigations, it seems logical to conclude that data so collected would be more trustworthy than that obtained from captive specimens. Accordingly, only such evidence obtained from the field will be presented. Activity of captive voles lends support to the conclusions and validity of field investigations.

Trapping records, which form the lesser portion of the evidence, were made over a period of five years (1932-1936). Snapback traps, which kill the mice, and Sherman metal traps, which take them uninjured, were used throughout the study. If snapback traps are placed directly in the runway of the mice, they are readily caught. Disturbance of the grass when setting the traps will often start the mice from their retreat. Accordingly, an undue proportion is frequently taken during the placing of the traps and does not give a true index to normal activity. Thus mice caught within an hour of the setting of the snaptraps were omitted from the calculations.

The most trustworthy figures may be secured only when traps are not placed directly in the runways, but rather to the side. Sherman box-traps were placed at right angles to the runways, the opening flush with one side of the beaten paths frequented by these voles. During periods of heavy snow, traps were placed at vantage points marked by clumps of orchard grass (*Dactylis glomerata* L.) where the snow tunnels frequently converge. When deep snow persisted, the excavation was covered with cardboard or paper and held in place with snow or ice.

Oatflakes were used for bait throughout the investigation. *Microtus* takes this food readily. It forms one of the staple dry foods of captive individuals, although Elton, Ford and Baker ('31) found that *Microtus* was not readily attracted by bait.

Studies on activity and home range of these mice were all conducted in the Ithaca, New York, region.

EVIDENCE OF TIME OF ACTIVITY

From spring of 1933 until fall of 1936 population studies were conducted. Orchards, alfalfa and timothy fields, and vacant lots grown to a mass of weeds and grasses were all investigated. Thirteen areas, more or less delimited by natural boundaries, were selected early in the investigation. Approximately

4,000 mice have been taken dead, of which reasonably exact data on time of capture are available on 1,400. Table I indicates the nocturnal and diurnal captures of mice over a three year period. Approximately half the sets were made in the early morning, the rest usually made in late afternoon. Thus, time of setting had no apparent selective effect on captures.

TABLE I. *Time of capture of 1385 mice in snap traps*

Period	Average possible hours of sunshine per day	Captures		Per cent taken during day
		Day	Night	
October-March, 1933-36	10.3	369	216	63.1
April-Sept., 1933-36	14.0	582	218	72.7

More accurate data are presented in figure 1, which is based on a large number of mice taken alive in Sherman metal traps. If the traps are placed at feeding centers, or to the side of the runway, the mice enter voluntarily.

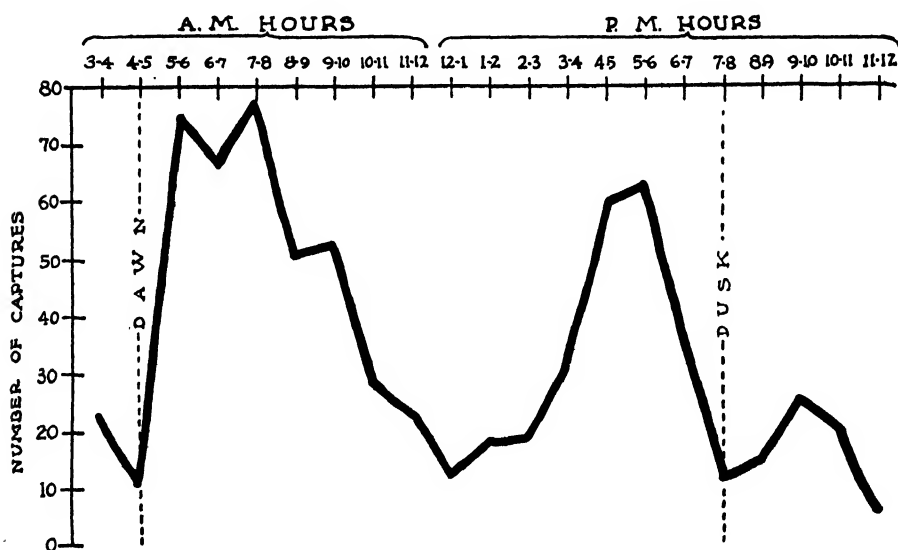


FIG. 1. Period of activity of field mice as determined by captures in Sherman metal box traps. The traps were placed at side of runways and baited with oatflakes, thus the mice entered voluntarily.

They may be immediately released, after marking, in the same situation where they were captured. Such trapping does not frighten the mice unduly, for individuals have been retaken more than a dozen times during the course of a month. Care should be exercised to provide the captured mice with grass during cold weather. Similarly, the traps become very hot in summer, and unless covered with weeds and grasses, the mice will die in a short time.

Traps were visited on the hour. Hence it was impossible to state whether the mice had been in the traps for 5 or 50 minutes. This is of slight importance, for an attempt was made only to gather data bearing on the approximate time of activity. Figure 1 indicates that an apparent lull in activity precedes dawn, and increasing activity is manifest from one to three hours after dawn. A lull in activity at mid-day is followed by renewed energy in the late afternoon. About dark, when crepuscular species are most active and nocturnal forms are starting abroad, field mice are relatively inactive. Little movement is indicated at midnight.

Another and more accurate method of determining periodicity of activity in field mice was tried. Acceptable baits were placed at vantage points in the runways of the mice. The bait stations were marked with numbered stakes, and the hours when baits were removed or eaten by mice recorded. Such ob-

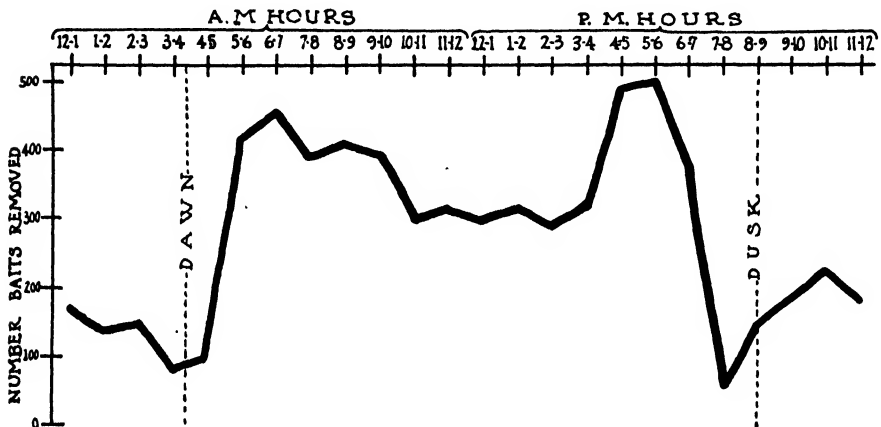


FIG. 2. Period of activity of field mice as determined by removal of baits (oatflakes, apple and carrot), indicating greatest activity in early morning and late afternoon.

servations in any one area were not recorded for longer than 24 hour periods at a time, thus obviating the likelihood of mice becoming unduly attracted to the baits and making regular trips to such stations. Oatflakes proved the most desirable, but had the disadvantage of becoming unattractive when moistened by even a light shower. The flakes proved attractive to crickets, which took a certain share. Their manner of feeding and the residue were characteristic, and indicated what baits had been disturbed by these insects. Small pieces of apple and carrot, the size of a marble, were likewise used. The frequent disappearance of such baits demonstrated their value in the study. In order to maintain a fresh supply of such baits and keep them palatable, new baits were set out at hourly intervals. The apple and carrot proved to be particularly desirable as they were not disturbed by other animals.

The observations point to greater activity by day than by night. There is indication of considerably greater activity shortly after dawn and in the late

afternoon, although the figures clearly connote some activity at all hours. The experimental data agree surprisingly well with the general observations made on *Microtus montanus yosemite* by Howell ('24) who says, "... and they were certainly most active for a couple of hours before darkness and again for an hour or so after sun-up, probably on account of the copious dew at this spot. There seemed to be comparatively little activity during the middle of the day or middle of the night, judging by the condition of the specimens caught."

Undoubtedly a number of factors operate which determine the movements of mice. Feeding activity, in response to stomach contractions, probably actuates movement. Richter ('27) has shown these contractions, in the rat, to be rhythmic. Predation probably plays some selective part in determining activity. The field mouse is the most prolific of any mammal, and its numbers play an important part in the food of a host of predators. Owls, weasels, foxes and skunks are active largely at night; hawks, crows, shrikes and snakes pursue their prey largely by day. There is a normal lull in the activity of these enemies for a short period preceding nightfall. Taking advantage of these periods would greatly lessen predation and enable the rodents to better maintain their numbers.

Density of cover seems to play little or no part in the movements of voles. A similar rhythm was noted when conducting trials both in fields offering an impenetrable cover of grass and weeds, and in areas which had recently been mowed, leaving sparse cover and the mice, accordingly, open to predation.

HOME RANGE

Little exact information has been recorded on the home range of small mammals. The little available data are largely conjecture; thus Seton ('09) supposes the home range of *Microtus drummondi* as "probably less than 50 feet across. I have seen an isolated hollow of that size which was obviously the whole world of a dozen or more of these mice." A tendency to wander was noted by Harper ('29) who found seven individuals in a grassy space "in the midst of a very extensive forest . . . an illustration of its ability to spread widely and to occupy small and well-isolated areas of favorable environment." *Clethrionomys*, a microtine congener of *Microtus*, is indicated by Townsend ('35) as having a limited home, for individuals were retaken in the same place as originally captured. A small home range for *Peromyscus* has been recorded both by Johnson ('26) and Murie and Murie ('31). Unpublished observations of the writer suggest a home range in the deer mouse not in excess of a quarter acre.

In limiting the range of a species, an area sufficient in size must be selected which will give the species ample opportunity to range widely. Accordingly, suitable areas from 3 to 10 acres, well populated with mice, were chosen. The center of such areas was selected (a portion usually approximating an acre) and mapped. Numbered stakes were placed at intervals

of 3 to 5 yards. Before the study of any one area had been terminated, trapping had been conducted on the entire area. When the mice were collected, they were removed from the trap, placed in a fruit jar and etherized. In etherizing small rodents, great care must be exercised, and the animals speedily removed from the jar when movement ceases, otherwise death will occur. The mice were marked by removing one or more toes. Thus the outside toe on the right fore foot is 1, the next 2, the inner 4, the outside toe on the left fore foot 8. Each toe on the hind feet, commencing with the outside toe on the right hind foot and ending with the similar member on the left hind foot, may be numbered, consecutively, from 10 to 100. Omitting the numbers ending in 9, it is thus possible to mark the animals from 1 to 108, or a total of 98 in any one area. Further combinations enable the investigator to use considerably higher numbers, and thus mark a greater number. The animals are weighed, sex determined, breeding condition of the females, time of capture, etc., noted. The animals are then liberated where caught, or if homing behavior is to be determined, liberated at any selected place. During the period from 1934–1936 more than 600 mice were thus marked. Data on more than 100 repeated captures are available, and give a fair index to the home range of the animal. A few typical case histories are listed:

Number 8. An adult 50 gram male was taken at Station 1 on June 16, 1936. It was marked and liberated at the point of capture. On June 28 it was recaptured at Station 6, 81 feet south of Station 1. The mouse was liberated at the second place of capture. The following day it was retaken at Station 27, 42 feet east of Station 1. On July 24 the mouse was captured at Station 3, 28 feet south of Station 1. The next day the specimen was caught at Station 25, 36 feet southeast of Station 1. On October 1, 1936, the mouse was taken at Station 1, the original point of capture $3\frac{1}{2}$ months earlier.

Number 14. A young male, about two weeks old, was captured on May 23, 1936, at Station 28. On June 10, it was taken at Station 19, 270 feet south of Station 28. On June 16 it was retaken at the same place. Ten days later the mouse was caught at Station 18, 13 feet south of Station 19. A month later it was retaken at Station 18. Recaptures on August 2, August 21 and September 11 were at Station 19, indicating the home range was localized, for it had opportunity during this period to enter neighboring traps, set a few paces north and south of 19.

Number 17. An adult gravid female, collected on May 23, 1936, at Station 29, was recaptured on May 30, 16 feet south of Station 29. The following day it was trapped 34 feet southwest of 29, while on June 10 the mouse was retaken at the original point of capture. On June 16 it was captured at Station 3, 30 feet west of the last point. On June 28 it was taken 15 feet south of Station 3. The following day I took this mouse 32 feet south of Station 3. It was recaptured on June 30 at Station 27, 30 feet

south of the point of its first capture. It remained about this point for some time, for it was taken in the same trap on July 20, July 24, August 2, August 29 and September 7. Over a $3\frac{1}{2}$ month period the mouse was repeatedly caught in an area encompassing less than 1200 square feet. It apparently did not wander from this area, for there were traps set rather closely all about the field bordering this small area. During this period the mouse produced 3 litters of young, and had a fourth well under way when last recaptured.

Number 22. A large female was taken in a mat of quack grass on November 16, 1935. The following day this mouse was retaken in the same trap. On November 20 she was captured at Station 11, 6 feet south of the first point. On November 23 the mouse was retaken at Station 11. One week later she was caught at Station 20, 34 feet west of Station 11 and 32 feet west of Station 10.

Number 35. An adult male captured at Station 55 on October 3, 1935, was recaptured on October 9 at Station 56, 40 feet south of its previous capture. On October 16, 29, November 2, 16, and 23 the mouse was retaken at distances varying from 9 to 20 feet from its point of capture on October 9, indicating a home range not greatly in excess of 1,200 square feet.

Number 52. A young female was captured on June 16, 1936, at Station 5. She was again taken at this point on June 29, July 2 and July 3. July 5, 20, 22 and 27 found her at distances not exceeding 30 feet from the original point of capture, and suggests a very restricted home range, possibly not exceeding $1/40$ of an acre.

Number 98. An adult female was taken on April 16, 1935, at Station 47. A week later the mouse was recaptured 6 feet east of Station 47. On April 30, May 1, 16 and 29 she was taken at 47, while on June 20 the mouse entered a trap 8 feet south of 47. Seven times during the summer she was recaptured, in no instance more than 28 feet from Station 47.

The larger number of more than 100 mice that were retaken more than once were trapped in large grassy plots. Well defined runways existed in such habitats. It is conceivable that, where suitable cover is lacking, or present only in long strips barren on either side of food and shelter, that the mice might foray more widely. Those who have watched field mice dart through the grass, moving so fast that nothing more than a streak of brown is visible, and running for a hundred feet at a time, might well question the data recorded above. It is likely, however, that these rodents leave a restricted home range only under duress, and will travel more widely when harassed by an enemy.

The results of this study point to a very limited home range, even in extensive areas of similar habitat. Males wander more widely than females, and are more likely to take up residence in new areas which have been previously unpopulated by the species. This is in keeping with the "wandering tendency" theory proposed by Townsend ('35).

HOMING BEHAVIOR

Many mammals exhibit a "homing instinct" or "sense of direction." The studies of Murie and Murie ('31) with the deer mouse, *Peromyscus maniculatus artemisiae*, proved that these mice returned to their home sites when released at distances varying from several hundred yards to two miles. In the Ithaca, New York, area, the writer has repeatedly had deer mice, *P. leucopus noveboracensis*, return to a three acre hardwood stand, when removed distances varying from one-quarter to one mile. Indeed the mice return to the same stump from which they were originally captured.

While only limited data are available on the homing behavior of *Microtus*, these indicate that the species, when removed 250 to 500 yards from the point of capture apparently failed to return, acquiring new home sites and territory in the general area in which they were released.

During June 1935 an adult male was repeatedly taken in an area encompassing not more than 2,000 square feet (approximately two-thirds the area of a tennis court). On July 25th the animal was trapped and released at 4 P.M. some 220 yards north of this area. At 7 A.M. of the following day the mouse was recaptured in its home territory. It was again removed 200 yards south of the area and liberated at 8:20 A.M. At 9:30 A.M. it was recaptured in the original habitat. The microtine had thus travelled 200 yards on its return trip in an hour or possibly less. The same day the individual was returned to a point 250 yards north of the home area. Five hours later it was taken at a point almost midway between its original point of capture and the station where it had been released. The mouse, after liberation at this last point of capture, was not retaken.

An adult female, during May-July 1936, was retrapped time after time in an area not greater than 3,000 square feet. This mouse was removed a distance of 150 yards and released on July 24, 1936. Nine days later it was recaptured in its original range. The mouse again returned to its home site when removed in different directions to distances varying from 100 to 250 yards. When released 350 yards from the original range, the mouse was not recovered. Apparently it had set up quarters in a new locality.

A large male resorted to an area perhaps 3,000 square feet in extent. On July 20, 1936, the mouse was removed a distance of 250 yards. Four days later it was taken at the original place of capture. Again it was transported to an area 200 yards off. It returned to its home site in less than 20 hours. When removed to an area of suitable cover 300 yards distant, the mouse apparently established new quarters, for it was taken twice in this new area in the space of a week.

The reader should not gather from these histories that there exists a specified distance in which field mice can or cannot return to their normal home range. It is quite clear, however, that the homing behavior of *Microtus* does not operate over as great a distance as that of *Peromyscus*.

SUMMARY

Voles are more active by day than by night. The period of greatest activity occurs shortly after dawn and in the hours preceding dusk. Predation possibly plays a selective part in determining periods of greatest activity, for less activity on the part of vertebrate enemies is apparent during early morning and late afternoon. The home range of an individual vole seldom encompasses an area in excess of 1/15 of an acre. "Homing instinct," while not developed as well as that in some cricetine rodents, nevertheless permits *Microtus* to return to its home range when repeatedly liberated at distances varying from one hundred to two hundred and fifty yards.

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THE FOREST SOIL OF THE DOUGLAS FIR REGION, AND CHANGES WROUGHT UPON IT BY LOGGING AND SLASH BURNING

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The need for a greater knowledge of forest soils is becoming increasingly evident in the United States as forestry approaches a management basis. In the Douglas fir (*Pseudotsuga taxifolia* (LaMarck) Brit.) forest region of the Pacific Northwest, where logging is usually followed by broadcast burning, information is needed not only as to soil composition and the soil disturbance resulting from logging but also as to changes in soil conditions resulting from fire, as it is very evident that the ecology of the site is materially changed by burning. Although considerable effort has been devoted to study of the soils of cultivated valleys in the Pacific Northwest, comparatively little research has been done on the true forest soils of this highly productive forest region.

SOILS OF THE REGION

The region's forest soils represent all its many soil types, and thus vary widely both in texture and in other characteristics. The textural classes include all variations from gravel to heavy clay; the most common or characteristic soil of the region is a loam. The mineral soils of the more rugged areas, which will likely be retained as forest land, are in general of poorer quality and coarser texture than those of the agricultural lands. On certain areas the weathered portion of the soil is characterized by the presence of shot-like iron-cemented pellets. Soils having this characteristic are often spoken of as shot soils, shot loams, and shot clays.

One of the soil groups most prevalent in the southern part of the Douglas fir region (Mangum, '13) consists in residual soils derived principally from basaltic rock and to a lesser extent from sandstones, shales, and other rocks. Large tracts of alluvial soil occur in the region; and although much of this type has been given over to agricultural use, it is still an important forest soil. Sedimentary gravels, sands, and silts are present, particularly in the northern Cascade Range and Puget Sound Basin, where many of the timberland soils are of glacial origin. Small areas of volcanic-ash soil are found in the higher mountains toward the eastern limits of the Douglas fir region. These mineral soils vary in thickness from a thin coating on rocky surfaces to unmeasured depths in the alluvial valleys.

The soil profiles of the region, although bearing a general resemblance to

each other, exhibit local variations because of differences as to parent rock, climate, drainage, and plant cover.

Soil type, the texture and character of the soil, is an important factor in the establishment and growth rate of forest trees. In relation to the establishment of the trees the characteristics of the surface layer, both mineral and organic, have greater significance than those of the subsoil.

Despite the great variation in tree growth that results from variation in soil and climatic conditions, over the greater part of the region the thickness of the layer of duff¹ is in general rather uniform, averaging about 1.5 inches. The thinness of the duff layer indicates that regional conditions favor decay, keeping decomposition very nearly in equilibrium with deposition. A heavier duff cover accumulates where decomposition is retarded by excessive moisture (in the coast country) or by shortness of growing season (in the high mountain country).

EFFECT OF LOGGING AND SLASH BURNING ON SOIL

The logging practice common in the Douglas fir region has been to clear cut the forests and to log with powerful donkey engines; this disturbs surface-soil conditions and leaves on the logged areas, in addition to the original duff layer, great quantities of slash (tree tops, branches, unmerchantable trunks, etc.). Figures compiled for several operations (McArdle and Isaac, '34) showed that the quantity of slash left on an acre after logging averaged 24,000 cubic feet, and that this average included 15,000 cubic feet of small branch wood, twigs, chips, bark, and slabs. Disposal of slash is required by the laws of Oregon and Washington, as a measure for reducing fire hazard. Broadcast burning has been the common method of disposal. A light slash fire has been found to destroy 90 per cent of the branch wood and about 10 per cent of the larger material. Although destruction of this material effectively reduces the immediate fire hazard, it deprives the soil of a protective cover and a future source of organic matter. Combustion of accumulations of slash such as are common in the region produces extremely high temperatures lasting for several hours.

Another important effect of fire is that it leaves the soil surface coated with black, charred debris. This increases the soil's capacity to absorb heat. At an air temperature of 85° F., for example, at which surface temperatures of yellow mineral soil may rise to 125° or higher, surface temperatures of black, charred soil may rise to 140° or higher (Isaac, '29). On the plots where these temperature relations were observed, a soil temperature of 135° killed

¹ Although "duff" as defined by the Society of American Foresters applies only to that portion of the forest floor intermediate between the litter (the upper, slightly decomposed portion) and the humus (the portion in which decomposition is well advanced), in this study the term has been applied to the forest floor as a whole. This was done because in taking samples for analysis it was impracticable to differentiate between layers of the forest floor. Duff is here classed as a part of the soil.

16 per cent of a stand of Douglas fir seedlings that had germinated within the preceding 8 days, and one of 143° killed 47 per cent of a stand that had germinated within the preceding week; in another case (McArdle and Isaac, '34), heat deaths of Douglas fir seedlings less than a week old were observed to result from a surface-soil temperature of about 123°.

Still another effect of slash fire, which has often been noted but until recently² was never evaluated in this region, is the change in the fertility, structure, and moisture-holding capacity of the soil, brought about largely through destruction of organic matter at the soil surface and in the upper portion of the mineral soil.

Observations made on cut-over land in the Wind River Valley, Washington, which led to the present study, showed that changes in soil caused by slash fires had a deleterious effect on survival in a plantation of Douglas fir, and that this effect was most serious where the fire had been hottest. Seedling survival was particularly low on spots where several logs had been burned together and where consequently the surface soil had been reduced to a red ash. Rain falling on such soil puddled the surface, reducing its capacity to absorb water; as a result, such spots dried out quickly. Samples of mineral surface soil from heavily burned areas and from adjacent areas burned lightly or not at all were analyzed by soil scientists of the Washington and Oregon State Colleges. In the reports on the analyses it was stated that the heavily burned soil showed depletion of the nitrogen supply, breakdown of the colloidal structure, dehydration of the secondary minerals present, and a more or less complete destruction of organic matter; that restoration of the nitrogen supply and organic matter would take many years, although weathering would probably restore the structure of the mineral soil to its former state almost entirely within five years. This estimate has been sustained by the results of later plantings: survival of replacements increased annually up to the fifth year, when practically all replacements survived; but even in their tenth year Douglas fir seedlings on heavily burned soil are not making good growth, and their foliage is of a sickly yellowish color contrasting strikingly with that of the foliage of seedlings on adjoining soil not heavily burned.

² The field work of the study discussed here was done in 1932. During the summer of 1933 a study of the effect of burning on Douglas fir forest soils was made by Fowells and Stephenson at Oregon State College. These investigators stated their conclusions as follows: (1) "Nitrification in forest soils is stimulated by burning and the liberation of the basic ash materials." (2) "Burning and the increased nitrification increase the soluble mineral nutrients in the soil, probably for some time after burning." (3) "Burning destroys not only the organic matter on top of the soil, but may destroy some of that in the immediate soil surface." (4) "The temporary effect of burning may be helpful at least in some respects, but, since the productivity of the forest soil depends upon gradual mineralization of the fallen litter, it does not appear reasonable to expect continuous and often repeated burning to improve forest soil fertility."

STUDY OF WIND RIVER VALLEY SOIL

In order to arrive at a more complete knowledge of Douglas fir forest soils and a more definite quantitative statement of the changes wrought in them by burning, in 1932 a cooperative study of a soil typical of the region was begun by the Pacific Northwest Forest Experiment Station and the soils section of the Washington State Agricultural Experiment Station.³

The area upon which the study was made is a comparatively level but well-drained terrace on the Wind River Experimental Forest, near Carson, Washington. On part of the area the mature Douglas fir timber had been cut in 1931, but the slash had not been burned. In the autumn of 1932, when the moisture content of the mineral soil and duff was somewhere near the low point for the year, mineral-soil and duff samples were taken at points where the slash covering was heavy and at points where it was light. Each point at which a sample was taken was marked with an iron stake. When rains began, a month later, the slash was burned broadcast. Temperatures of the slash fire were measured just above the duff surface and 1 inch below it, by means of a pyrometer and thermocouples. The highest temperatures recorded above and below the duff surface, respectively, were 1,841° F. and 608° F. (The latter was recorded in a mixture of duff and mineral soil.) These temperatures occurred at one of the points where the slash was heaviest. Where the slash was lighter, temperatures were lower. After the fire, samples were taken at approximately the same points and also from the duff under the old-growth timber.

As rotten logs often form a part of the soil stratum for growth of some forest trees, especially western hemlock, *Tsuga heterophylla* (Raf.) Sarg., samples of this material, also, were taken.

General description of soil

The mineral soil of the study area, a member of the Wind River Series (Mangum, '13), is of nonglacial, alluvial origin, derived principally from basaltic rocks. When moist it is of a light chocolate or tan color; when dry it is of a lighter color, with a yellowish tinge. Upon ignition it turns brick red. Its structure is moderately open and friable.

After thorough air drying, a mechanical analysis of the mineral portion of the soil gave the results shown in table I. Approximately 37 per cent of the material failed to pass through the 2-millimeter screen. This coarse material was made up largely of iron-cemented accretions of completely weathered soil particles. The material that did pass through the screen contained such percentages of sand, silt, and clay that it was classed as a sandy clay loam.

³ The soil sampling and slash burning were done by the senior author. The analytical work was performed (and reported in a senior thesis) by the junior author, under the direction of L. C. Wheating, in the laboratories of the soils section, Washington State Agricultural Experiment Station.

TABLE I. *Mechanical composition¹ of the mineral portion of Wind River soil*

Depth of sample (inches)	Coarse material %	Fine material %		
		Sand	Silt	Clay
0 to 3	38.4	58.5	18.1	23.4
3 to 6	40.8	56.4	19.4	24.2
6 to 12	40.1	52.2	21.8	26.0
12 to 36	28.1	53.8	29.9	16.3

¹ As determined by the Bouyoucos hydrometer method. Coarse material = more than 2 mm. in diameter; sand = 2.0–0.05 mm.; silt = 0.04–0.005 mm.; clay = less than 0.005 mm.

The fire produced no measurable effect upon the texture of the soil. It greatly altered the structure of the surface layer, however, through elimination of organic matter, breakdown of colloidal structure, and deposition of ash.

Where the forest floor of the study area had not been disturbed there was present a duff covering that averaged about 1 inch in thickness. This covering was made up of three rather indistinct layers: A thin top layer of recently deposited fine litter; a thicker middle layer of more compact, decomposing organic matter in which the form of the original material (needles, leaves, herbaceous stems, twigs, cones, and bark scales) was still discernible, although decreasingly so from the surface down; and a very thin layer of crumbly, black, amorphous humus in mixture with mineral soil. In addition to the duff proper there were found on the area at frequent intervals stubs and logs in all stages of decay.

Organic content and total Nitrogen content

As soil constituents organic matter and nitrogen are both of major importance, and bear close chemical and biological relations to each other. The organic content of soil, in addition to other relations, in part determines its moisture-holding capacity. Organic matter occurs primarily in the duff but is found also, in smaller quantities and in a more completely decomposed form, in the mineral soil. Nitrogen is present in soils mainly as undecomposed organic nitrogenous compounds; it occurs in smaller quantities in the simpler and more available products of organic decomposition—nitrates and ammonium compounds.

Quantity of organic matter was calculated for the samples of duff and rotten logs from loss on ignition, and for the mineral soil samples by the Degtjareff-Schollenberger chromic-acid method. Total nitrogen was determined by the Kjeldahl method. The organic-matter content and the total nitrogen content in percentages of dry weight, and the nitrogen-carbon ratio of the soil before and after slash burning, are shown in table II.

The average nitrogen-carbon ratios before burning, 1:57 for duff and 1:24 for mineral soil, were broad in comparison with that commonly found for agricultural soils, approximately 1:10. The average nitrogen-carbon ratio for crumbly, rotten log material was 1:168.

TABLE II. *Organic content, nitrogen content, and nitrogen-carbon ratio of Wind River soil before and after a heavy slash fire*

Sample	Organic matter % ^{1, 2}		Total nitrogen % ^{1, 2}		Nitrogen-carbon ratio	
	Before fire	After fire	Before fire	After fire	Before fire	After fire
Cut-over area						
Duff	88.53	9.72	0.92	0.34	1 : 57	1 : 17
Rotten log	98.62	—	.29	—	1 : 165	—
Mineral soil at depth of—						
0 to 3 inches	5.69	3.54	.12	.12	1 : 27	1 : 18
3 to 6 inches	3.72	3.13	.09	.10	1 : 24	1 : 18
6 to 12 inches	3.40	2.79	.09	—	1 : 22	—
12 to 30 inches	2.21	2.48	.06	—	1 : 21	—
Adjoining old-growth timber area						
Duff	78.7	—	.87	—	1 : 52	—
Rotten log	97.4	—	.33	—	1 : 171	—

¹ In terms of dry weight of soil.

² Calculated for duff and rotten logs from loss on ignition, and for mineral soil by the Degtjareff-Schollenberger chromic-acid method (the quantity of organic carbon being multiplied by the factor 1.724).

³ As determined by the Kjeldahl method.

Calculations based on figures presented here and on additional information obtained showed that before burning there was present on the average acre of the study area a total of 32 tons of duff; that approximately 28 tons of this duff was organic matter, containing 594 pounds of nitrogen; and that the slash fire consumed 25 tons of this organic material (exclusive of the rotten logs) and drove off approximately 435 pounds of the nitrogen. This is as much nitrogen as would be taken off by the removal of 112 cords of wood, or by the total grain-crop removal from cultivated land for a period of 15 years. It is recognized that some of this nitrogen would have been lost through the ordinary process of decomposition of organic material over a period of years; but the quantity that had accumulated and was present when the area was burned is evidence that the ordinary loss of nitrogen in the process of decomposition of organic material is more than offset by the accumulation of nitrogen from various sources.

After the fire the nitrogen-carbon ratio was narrower, because the decrease in organic carbon was proportionately greater than the decrease in total nitrogen.

The figures given for nitrogen content of duff before fire (0.92 per cent for the cut-over area and 0.87 per cent for the old-growth timber area) do not differ greatly from those reported by Alway, Kittredge, and Methley ('33) for the forest floor of old-growth jack pine, *Pinus banksiana*, and Norway pine, *P. resinosa*, stands in Minnesota unburned for 50 years. In the litter, duff, and leaf mold these investigators found a nitrogen average of 1.07 per cent in jack pine stands and one of 0.97 per cent in Norway pine stands.

In the longleaf pine, *P. palustris*, forest region Heyward and Barnette ('34) found that on eight areas sampled the nitrogen content of burned soil averaged 0.0493 per cent, whereas that of unburned soil averaged 0.0521 per cent, and that for two of the areas the difference was significant. They found also that on five of the eight areas loss on ignition (used as a measure of organic content) was greater for the burned soil. Their study cannot be compared directly with the Wind River study, for two reasons: (1) The eight subareas they classed as unburned had all been burned within 44 years, six of them within 20 years and four of them within 11 years; and (2) the samples analyzed, instead of including the litter and the duff proper as did those taken in the Wind River study, were all taken from the *A* horizon, that is, the surface soil layer underlying the litter and the duff proper.

Working on the pitch pine plains of southern New Jersey in the years 1929-32, Lutz ('34) found evidence that prior to 1923 areas known as the "pine barrens" had been burned on the average at least once every 16 years and areas known as the "plains" had been burned on the average at least once every eight years. He found that the soil of the surface (0-10 cm.) layer was lighter on the pine barrens than on the plains. He found also that on the pine barrens as compared with the plains the nitrogen relations in the surface soils were slightly more favorable and the organic carbon content of the mineral soil greater.

Waksman and collaborators have remarked ('28) that "the nature of the fixation of nitrogen in forest soils . . . has remained very vague, since neither *Azotobacter* nor legume bacteria are found to occur to any extent in these soils, especially in the 'raw humus' soils." Such observations as have been made in this field suggest that fixation takes place slowly at best, and that loss of nitrogen in such quantity as is shown in this study must be considered a serious matter. It has been suggested that most of the nitrogen present in the soils of coniferous forests has been deposited in the precipitation. According to all available figures on the subject, such deposition is an extremely slow process. Shutt ('17) reports that in the neighborhood of Ottawa, Canada, during the 10-year period ending with February 1917, an average of 6.583 pounds of nitrogen per acre per year, in the form of free ammonia, albuminoid ammonia, nitrates, and nitrites, was brought to earth by precipitation averaging 23.39 inches per year. At this rate 66 years' precipitation would deposit no more nitrogen than was lost in one slash fire at Wind River.

Moisture relations

Aside from nitrogen relations, the organic matter of the soil has great significance because through its influence on soil texture it governs that most important property of any soil, moisture-holding capacity.

Soil moisture controls plant growth through its function as a solvent and carrier of nutrients, its direct function as a nutrient, and its numerous relations to chemical processes and microbial activities in the soil. In the Douglas

fir region the availability of water near the surface of forest soil is especially important after timber is cut, because of the high moisture requirements for germination and early seedling development.

Maximum moisture-holding capacity of the soil of the study area was determined by placing a thin layer of the dry soil (of known weight) in a perforated cup, saturating the soil, allowing it to stand until moisture ceased to drop from the cup, and comparing the weight of the saturated soil with the weight of the dry soil. Field moisture-holding capacity was determined by soaking a similar sample and then subjecting it to a suction force of one-half vacuum (negative pressure of 15-inch mercury column). The results are shown in table III.

TABLE III. *Maximum moisture-holding capacity and field moisture-holding capacity of Wind River soil, in terms of percentage of dry weight of soil, before and after a heavy slash fire*

Sample	Maximum capacity %		Field capacity %	
	Before fire	After fire	Before fire	After fire
Cut-over area:				
Duff	407	212	190	60
Mineral soil at depth of—				
0 to 3 inches	98 ¹	92 ¹	75	50
3 to 6 inches	87	90	43	55
6 to 12 inches	97	86	50 ¹	57 ¹
12 to 30 inches	94	88	61 ¹	79 ¹
Rotten log	403 ¹	—	246 ¹	—
Adjoining old-growth timber area:				
Duff	512 ¹	—	278 ¹	—
Rotten log	448 ¹	—	286 ¹	—

¹ Figures based on samples from one location. The other figures are based on samples from two locations.

It is recognized that maximum soil moisture-holding capacity varies with thickness of soil layer and with compactness of soil; data on maximum capacity are presented here only as showing the total quantity of water that soil can hold for a short period after a rain.

Variation in character of soil within very short distances may account for such small differences in moisture-holding capacity before and after the slash fire as are shown for depths of 3 to 30 inches; but the differences shown in the moisture-holding capacity of the duff and in the field moisture-holding capacity of the 0-3-inch layer of mineral soil are so great as to form unmistakable evidence of loss by fire such as would seriously affect seedling survival.

The high water-holding capacity of the duff and of rotten wood constitutes one of the striking features of these results.

According to the data presented in table III, the 25 tons of duff per acre that was destroyed by the fire had a maximum moisture-holding capacity of approximately 1 inch of rainfall; that is, under undisturbed conditions it

would have retained this quantity at the time of fall and released it gradually over a long period. (The moisture-holding capacity of the rotten logs consumed and of the organic matter removed from the 0-3-inch soil layer by the fire was not computed on an acre basis in terms of rainfall.)

While no absorption tests were made in connection with this study, burning is known to reduce the absorptiveness of forest soils. Auten ('34), in a series of tests in the Ozark highlands, found that the rate of water absorption per square foot of soil was 6 to 8 times as great in unburned forests as in burned forests.

Soil reaction

Burning of the duff layer and deposition of the ash on the surface effect a change in the duff, shown in table IV, from a highly acid condition to an alkaline condition. The change in reaction is possibly one of the most significant immediate changes brought about by fire in the soil factors affecting tree growth. Degree of acidity functions both through its controlling influence over chemical changes and biological activities in the soil and through the direct effect on the plant of excessive quantities of acids or basic salts. Thus it may have an important bearing on both type and quantity of vegetation.

TABLE IV. *Reaction of Wind River soil before and after a heavy slash fire*

Sample	Reaction ¹	
	Before fire	After fire
Duff	<i>pH</i> 4.95	<i>pH</i> 7.6
Mineral soil at depth of—		
0 to 3 inches	5.0	6.2
3 to 6 inches	4.8	5.5
6 to 12 inches	5.0	4.9
12 to 30 inches	5.15	5.2
Rotten log	4.2	—

¹ Determined by colorimetric method.

Formerly it was considered that the action of nitrifying bacteria was inhibited in soils with a pH value of 5.5 or less. In recent experiments by Romell and Heiberg ('31), nitrification was found taking place in samples of duff as acid as pH 2.9. However, there seemed to be some correlation between reaction and nitrification.

A slightly acid soil reaction appears to be favorable to most kinds of plant growth; Douglas fir seedlings, however, have been noted in the Wind River nursery of the Forest Service to make equally good growth on slightly acid, neutral, and slightly alkaline soils. The sweetening of the soil or the higher concentration of plant nutrients resulting from slash burning, or a combination of the two, appears to stimulate greatly the growth of certain competing

forms of herbaceous vegetation such as *Epilobium angustifolium*, *Senecio vulgaris*, and *Pteridium aquilinum* during the first few years following a slash fire.

Considerable rain fell between the times when the "before fire" samples and the "after fire" samples were taken; presumably the change in acidity at the 3-6-inch depth was due to the action of rain in carrying alkaline salts down into that zone.

The evidence of highly acid conditions before the fire is comparable with results obtained by other workers. Mork ('27), working in Norway, recorded acidity values of pH 3.2 for rotting windfalls upon which spruce seedlings were growing; the value of 2.9 for duff recorded by Romell and Heiberg has been alluded to.

Mineral nutrients

To determine the mineral-nutrient content of the duff on the study area before and after the slash fire, ignition tests were made of samples of duff taken before and after the fire. The percentages of total ash, silicon dioxide, phosphorus, calcium, and potassium found in this duff are shown in table V, together with comparable figures for rotten logs and for duff under old-growth timber on the study area.

TABLE V. Quantity and composition of residue of samples of Wind River soil after ignition

Sample	Weight of ash, in terms of total weight of soil %	Silicon dioxide, in terms of total weight of ash %	Nutrients, in terms of total weight of soil		
			Phosphorus %	Calcium %	Potassium %
Cut-over area					
Duff					
Before slash fire	13.26	69.5	0.115	0.81	0.177
After slash fire	50.96	80.7	.121	1.80	.306
Rotten log ¹	1.38	57.4	.028	.17	.051
Adjoining old-growth timber area ²					
Duff	21.33	73.7	.122	.91	.198
Rotten log	2.58	64.9	.026	.41	.040

¹ Sampled before a slash fire that completely destroyed it.

² Not subjected to slash fire.

The original duff layer on the average acre contained approximately 76 pounds of phosphorus, 555 pounds of calcium, and 121 pounds of potassium. Table V discloses that mineral nutrients form a higher percentage of the duff samples taken after the fire than of corresponding samples taken before the fire; but when total quantity of mineral nutrients in the unburned duff layer is compared with total quantity of mineral nutrients in the remaining

ash layer, it is evident that part of the original supply has been removed. The presence of unmeasured variables prevents a definite quantitative statement of nutrient loss; however, the fact that the increase in concentration of nutrients is far from proportional to decrease in quantity of duff indicates that a considerable loss has occurred. Since smoke is made up largely of particles of solid material held in suspension, the possibilities of such loss are evident. Smoke analysis might lend some valuable information on the exact quantities carried off in this way.

Available nutrients

More important than total nutrient content of the soil, from the standpoint of immediate plant growth, is the quantity of plant food available in the soil at a given time. This is constantly changing, because of changes in chemical and biological soil conditions. Temperature, moisture, reaction, leaching and erosion, crop removal, and fires are among the factors determining such changes. The plant food available at a given time consists of those nutrient salts that are actually dissolved in the soil water or are readily water soluble and, in addition, some acid-soluble minerals.

TABLE VI. Quantities of water-soluble salts and of other plant nutrients¹ available in Wind River soil before and after a slash fire

Sample ²	Water-soluble salts ³		Nitric acid soluble salts ⁴							
	Before fire	After fire	Before fire				After fire			
			P	K	Ca	NO ₃ -N	P	K	Ca	NO ₃ -N
Duff	1,116	1,330	4	4	2	0	2	5	5	3
Mineral soil at depth of—										
0 to 3 inches	370	585	0	0	0	1	0	1	2	4
3 to 6 inches	365	345	0	0	0	0	0	1	0	0
6 to 12 inches	164	222	0	0	1	0	0	1	0	2
12 to 30 inches	82	142	2	1	0	0	2	1	1	0
Rotten log	486	—	1	2	2	0	—	—	—	—

¹ As determined through tests with 0.2 normal nitric-acid solution.

² The areas on which duff samples were taken had been heavily burned; each mineral-soil sample was a composite of a sample from a heavily burned area and a sample from a lightly burned area.

³ Parts per million.

⁴ Figures used symbolize quantity of salts as follows: 0, none; 1, a trace; 2, poor; 3, fair; 4, good; 5, excellent; 6, excessive. This scale is based on the quantities of available nutrients commonly found in good agricultural soils.

The water-soluble nutrients in samples of Wind River soil were extracted by leaching the soil with distilled water, and were determined quantitatively by use of the Wheatstone bridge. The parts per million of water-soluble salts found are listed in table VI.

To determine total quantity of plant food available, investigators have

utilized various solvents supposed to simulate the action of plant roots in dissolving minerals. For this use 0.2 normal nitric acid has been shown to have certain advantages over other solvents tested. A nitric-acid extract of the samples was made and examined microchemically (qualitative tests) for the presence of phosphorus (P), calcium (Ca), potassium (K), and nitrate nitrogen ($\text{NO}_3\text{-N}$). The results are listed in table VI.

From this comparison it appears that prior to slash burning the mineral soil was deficient in all the plant-food elements, but that this deficiency was partially offset by a comparative abundance in the duff. Burning increased the supply of soluble salts, particularly at the surface and in the 0-3-inch layer. As a result of the fire a part of the nutrients contained in the duff as components of complex organic compounds, decomposition of which, in the absence of fire, proceeds slowly and probably renders the nutrients available over a long period of years, was deposited at the surface in highly soluble form. Part of the remainder was retained on the ground in unburned debris. A considerable part was lost; presumably, it was carried off in smoke. The increase of food elements in the 0-3-inch layer is attributed to the carrying down of materials by rain between the times of burning and sampling. The slash fire greatly increased the quantity of available calcium and measurably increased that of available potassium and nitrogen, but reduced the quantity of available phosphorus in the surface zones.

TABLE VII. *Results of three biologic tests upon composite samples of duff and the 0-3-inch mineral-soil layer before and after a heavy slash fire*

Test	Before fire	After fire
<i>Azotobacter</i> culture (comparative growth): ¹		
Soil alone	0	0
Soil plus phosphorus nutrients	0	4
Soil plus potassium nutrients	0	0
Soil plus calcium nutrients	0	0
Soil plus P and K nutrients	0	4
Soil plus P and Ca nutrients	4	3
Soil plus K and Ca nutrients	0	0
Soil plus P, K, and Ca nutrients	5	4
<i>Aspergillus</i> culture (weight of mycelial felt):	Grams	Grams
Soil plus P nutrient solution	0.830	0.961
Soil plus K nutrient solution	.949	1.110
Neubauer (seedling) test (quantity available in parts per million) for	Parts	Parts
Phosphorus	20	22
Calcium	30	53
Potassium	147	265

¹ The figures used symbolize growth as follows: 0, none; 1, a trace; 2, poor; 3, moderate; 4, good; 5, excellent.

To obtain more exact information upon quantity of nutrients available as affected by the slash fire, a more detailed study was made of composite samples of the duff and the 0-3-inch mineral-soil layer taken before burning and of corresponding composite samples taken after burning. The previous work

had shown that the effect of the burn was restricted almost entirely to these layers, and these layers are the zones of intensive feeding in the critical initial period. The samples taken were subjected to the three most favored biologic tests for available nutrients. The results obtained are shown in table VII.

Results of the test with the bacterium, *Azotobacter chroococcum*, indicated that burning had overcome a calcium deficiency for the growth of this organism in the soil, either by destroying organic acids or by depositing calcium in an available form, or by both. The fungus *Aspergillus* made better growth in both of the composite samples than it commonly makes in fair agricultural soils. (It made still better growth in unburned material in which the supply of potassium had been increased by direct addition of a potassium fertilizer or of burned soil.) Results of the Neubauer test, in which a chemical analysis is made of seedlings grown on a sample of the soil diluted with pure sand, showed strikingly that the fire had greatly increased the quantity of calcium and potassium available but had only slightly affected the phosphorus. This agrees with the results of the chemical tests on availability of nutrients.

A pronounced increase in available plant food as a result of slash burning is shown conclusively. In considering the probable effect of such an increase on establishment of Douglas fir reproduction, it should be borne in mind that under natural conditions the first year is the critical period for a Douglas fir seedling from the standpoint of temperature and moisture but not from the standpoint of adequacy of available plant food. However beneficial it may be in some other forest regions to have a greater than normal supply of plant food available in the surface soil during the first year of the regeneration period, in the Douglas fir region this condition may prove undesirable, since it tends to result in development of a luxuriant crown and a small, shallow root system. When the annual drought period occurs, a luxuriantly developed seedling crown is likely to transpire more moisture than the corresponding shallow root system can supply, with the result that the seedling succumbs to weather conditions in which a seedling with a smaller crown and a larger root system, such as develops on poorer soil, may well survive. Douglas fir seedling establishment in the Pacific Northwest, it is commonly recognized, takes place more rapidly on the poorer sites. A disproportion of crown to root system is particularly unfortunate in conjunction with the intensified drought conditions resulting from loss of part of the organic content of the soil by burning, a condition that cannot be expected to be remedied within the period (about 10 years) required for reseedling of cut-over Douglas fir areas.

How long increases in available plant food resulting from slash burning can be expected to last is not known. In the Douglas fir region, where winter rainfall is extremely heavy and the soil is highly subject to leaching,⁴ it seems unlikely that such an increase lasts beyond the first or second season. In this

⁴ At the Wind River Forest Nursery, adjacent to the study area, satisfactory soil fertility can be maintained only by plowing under a heavy cover crop after each crop of tree seedlings is produced.

region the more vigorous growth of fireweed, bracken, groundsel, and other weeds that occurs during the first one or two years after a slash fire is not matched in following years, and after each successive fire on an area the average height and vigor of weed growth is less. Alway and Rost ('28), working in Minnesota, reported that timothy sown on areas burned by the great Cloquet forest fire of 1918 made more vigorous growth the first year following the fire than timothy of older seedlings on nearby unburned fields. They reported also, however, that "a year later . . . the timothy in the burned woods had not made nearly as vigorous a growth that season as the older timothy on the nearby unburned fields. So in the second year it seemed the burning had reduced the productivity." A reduction of available nutrients below normal such as seems likely to begin in the second or third year following a slash fire is undesirable because of the effect on growth of established seedlings.

SUMMARY AND CONCLUSIONS

The soil of a typical Douglas fir forest in western Oregon or western Washington may be of any one of the many soil types found in the region, and unless it has been disturbed includes a layer of duff. The thickness of the duff layer averages about 1.5 inches; it is greater where decomposition is retarded by excessive moisture or by shortness of growing season. The mineral soils of areas in the Douglas fir region that are likely to be retained as forest land are in general coarse textured and of poor quality compared with those of areas now given over to agriculture. In this study of a typical Douglas fir soil, that of the Wind River Experimental Forest of the Pacific Northwest Forest Experiment Station, near Carson, Washington, analysis showed that the duff on the average acre, estimated to total 32 tons, contained approximately 28 tons of organic matter, 594 pounds of nitrogen, 76 pounds of phosphorus, 555 pounds of calcium, and 121 pounds of potassium. The duff has further significance because of its influence upon the soil's moisture-holding capacity and upon soil-reaction relations.

A Douglas fir logging operation commonly leaves on the ground a great accumulation of slash; figures compiled for several logging operations showed that the total quantity of slash per acre averaged 24,000 cubic feet, including 15,000 cubic feet of small branch wood, twigs, chips, bark, and slabs. Cutting and logging disturb surface-soil conditions. A light slash fire consumes about 90 per cent of the branch wood and about 10 per cent of the larger slash material. In doing this, while effectively reducing the immediate fire hazard it destroys a protective soil covering and a future source of soil organic matter. Combustion of accumulations of slash such as are common in the region produces extremely high temperatures lasting for several hours.

The usual heavy slash fire results in almost complete destruction of the duff layer. Involved in and associated with this destruction, on the particular area studied, were the following: (1) a loss per acre of 25 tons (89%) of

the organic matter contained in the duff; (2) a change in duff reaction, from a highly acid condition (pH 4.95) to an alkaline condition (pH 7.6); (3) the escape of approximately 435 pounds of nitrogen per acre; (4) an increase in the supply of plant nutrients available in the surface soil. This resulted from deposition at the surface, in highly soluble form, of a part of the nutrients present in the duff, which in the absence of fire would probably have become available gradually, over a long period of years. Serious subsequent losses by leaching appeared probable; and (5) an indicated loss of a considerable part of the mineral nutrients contained in the duff, presumably carried off in smoke.

The action of slash fire upon the surface zone of the mineral soil causes some dehydration of secondary minerals, colloidal breakdown, change from a favorable to an unfavorable structure, and reduction of moisture-holding capacity to a point at which seedling survival is seriously affected.

Blackening of surface soil greatly increases its heat-absorptive capacity, and can cause its temperature to rise high enough to kill tree seedlings at times when the surface temperature of adjacent unburned, natural-colored soil remains so low as to cause no injury to seedlings.

The greater than normal quantity of plant food available in the surface soil for a year or more after a slash fire may have an undesirable effect on Douglas fir regeneration. It tends to cause first-year seedlings to develop luxuriant crowns and small, shallow root systems, which unfit them for withstanding the annual summer drought. Drought conditions are made more severe by the reduction of the organic content effected by fire, and this reduction cannot be expected to be remedied within the period (about 10 years) required for re-seeding of Douglas fir cut-over areas. Unburned-soil conditions, in which normal quantities of plant food are made available gradually throughout the regeneration period, appear to be more favorable to Douglas fir regeneration. For this reason, and because of the adverse after-effects of fire on surface-soil temperature and soil moisture, two critical influences on initial establishment of Douglas fir, this study has led to the conclusion that the harmful effects of the ordinary slash fire more than outweigh any beneficial effects it may have on the productivity of Douglas fir forest soil. The study indicates further that the harm done is roughly proportional to the completeness with which the fire consumes the duff and the organic matter in the surface soil.

Since seedling behavior is the only certain measure of soil productivity, the foregoing conclusion can be positively substantiated (or reversed) only by actual checks of seedling establishment on burned and unburned portions of a homogeneous site. Such checks will be the next step in this study.

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THE VEGETATION OF A BAREFACED CLIFF IN WESTERN NORTH CAROLINA

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An extensive area of bare rock in otherwise wooded territory may often attract more attention than the surrounding forest. Barefaced cliffs are not at all uncommon in the southern Appalachians. Some, because of their extent and location, have become rather generally known. Whiteside Mountain, near Highlands, North Carolina, and Stone Mountain in Georgia are notable examples.

In the course of collecting trips in western North Carolina an area came to our attention which seemed of unusual interest. This barren outcrop is particularly striking because it is unusually steep, fairly extensive, and is surrounded on all sides by rich forest (fig. 1). The outcrop is in Jackson County, North Carolina, about six miles south of Tuckasegee, beside North Carolina State Highway 106 leading from Sylva to Glenville. The road here is at an altitude of approximately 3,500 feet. The granitic mass rises abruptly from the roadside at about a 45° angle and becomes even steeper in some parts. The exposure is southwesterly. At its highest point it extends upward some 300 feet to the hardwood forest which appears above on the decreasing slope. The widest extent of the exposure irregularly parallels the road for several hundred yards.

GENERAL CHARACTER OF THE VEGETATION

The rock surface is smooth with only slight undulations and is remarkably free of crevices, large or small. There is, consequently, little opportunity for the accumulation of soil or for root anchorage and vegetation develops in slowly formed mats only in the occasional hollows. These mats are in no sense permanent and are so poorly anchored that they cannot be depended upon to support one's weight when climbing. The organic debris at the base of the cliff is evidence of the fate of previous mats washed down by water or released by their own weight. Scattered mats of all sizes, however, do survive and, if they persist long enough, go through a progression of changes in species and growth-forms as they develop.

The development of vegetation on exposed rock is quite generally recognized as an extremely slow process. Cooper's ('28) photographic records for Isle Royale show no appreciable change among the pioneers over a period of seventeen years. Studies in widely separated areas (Braun, '16, '28, in

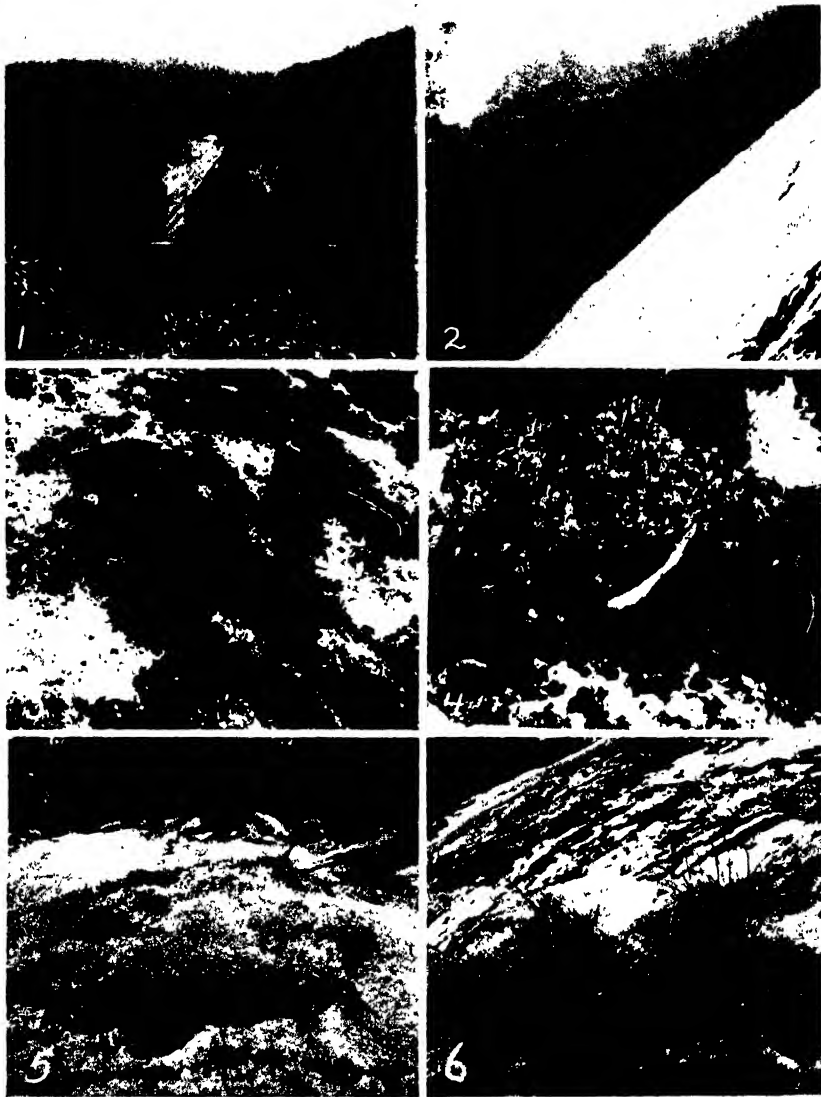


FIG. 1. The bare slope as seen from a distance. Smaller openings at the left and the main line of seepage is marked by the woody vegetation extending down the center.

FIG. 2. The bare rock showing the steepness of the slope, the smooth surface, and the absence of crevices.

FIG. 3. Colony of *Rhacomitrium heterostichum ramulosum* invading the bare rock surface.

FIG. 4. A mixed patch of *Andreaea rupestris* and *Rhacomitrium heterostichum ramulosum* with the lichen, *Cladonia subcariosa*, invading the mosses.

FIG. 5. A mat in which *Cladonia rangiferina* has practically eliminated *Selaginella* from the central area.

FIG. 6. *Danthonia spicata* and *Carex* sp. growing on the upper edge of a mat where mineral soil has accumulated.

Ohio; Cooper, '13, in Michigan; Nichols, '14, in Connecticut; Whitehouse, '33, in Texas) indicate a general uniformity in pioneer lichens and mosses with the later species contributing to, and appearing on, the mats which are formed. The importance of crevice species in anchoring the vegetation mats and thereby permitting the later stages of development is also well known. Cooper ('13) describes areas without crevices which had not progressed beyond lichen-moss mats although surrounding rock was clothed with climax forest. The absence of crevices combined with the steepness of the slope may possibly explain the scarcity of vegetation on this outcrop in an otherwise heavily forested section. It is probable that there will not be any conspicuous permanent development beyond pioneer bare rock species until weathering reduces the slope or crevices and hollows form where anchorage is favorable and soil can accumulate.

The steepness of the slope (fig. 2) the wide southern exposure, the absence of pockets and crevices all combine to make the habitat appear extremely dry. As might be anticipated most of the pioneer species are those adapted to survival in such precarious habitats. On larger mats, however, there is a surprising number of species which are normally found growing only in wet or boggy soils. All such mats are directly below seepage zones issuing from the forest above. Water drains from all the margin of the woods but as the excess is reduced the lines of percolation become more definite and in these places the mats are the largest and oldest. The highly organic soil absorbs water in quantity and retains it for days after a rain. During extended dry periods even the larger mats become quite desiccated and, there being only solid rock for a substratum, the vegetation suffers accordingly. A rather unexpected assemblage of plants fringes the woods at the top of the exposed rock. Here, seepage encourages the growth of a thick mat of mosses, predominately *Sphagnum subsecundum* Nees.¹ with *Thuidium delicatulum* Mitt., *Sematophyllum carolinianum* (C. M.) E. G. B. and the hepatic, *Scapania nemorosum* (L.) Dum., as well as clumps of *Thalictrum revolutum* DC., *Aletris farinosa* L. in abundance, *Scleria pauciflora* Muhl. and *Rhynchospora cymosa* Ell. scattered here and there. In late June the entire mat was dotted with *Calopogon pulchellus* (Sw.) R. Br. and scattered everywhere along the margins of the sphagnum was the little bladderwort, *Utricularia subulata* L.

SUCCESSIONAL STAGES ON THE CLIFF

Bare Rock Pioncers

Among the first plants to appear on any bare rock outcrop are crustose lichens. The importance of these plants as rock pioneers has been fully emphasized in the literature and it has been generally assumed that crustose lichens are universal pioneers in rock succession. Frye ('27) showed that

¹ The writers are indebted to Professor H. L. Blomquist for the identification of the sphagnums and to Mrs. Gladys P. Anderson for determining the lichens.

these lichens collect small amounts of soil and in certain cases aid in actual disintegration of the rock itself. Here they seem to be of little importance in aiding the later pioneers, although they are scattered abundantly over the area. Careful examination showed that early moss pioneers occupy the rock regardless of whether crustose lichens are present or absent and those which start on a patch of a crustose lichen apparently have no advantage over those coming in on the bare rock. Two mosses may be considered as pioneers for building up a mat of vegetation such as that referred to above. They are *Rhacomitrium heterostichum* (Hedw.) Brid. var. *ramulosum* (Lindb.) G. N. Jones (fig. 3), and *Andreaea rupestris* Hedw., both of which are common elements of the bare rock flora at high elevations in this region. Small plants of both species grow in minute crevices of the rock not previously occupied by any visible sign of crustose lichens and once a colony of either *Rhacomitrium* or *Andreaea* is established it slowly spreads on the bare rock in a more or less circular fashion. When a moss mat, spreading on the bare rock, comes in contact with scattered lichens and other mosses which may be present they are engulfed and finally eliminated. Apparently small amounts of soil which collect in crevices are sufficient for spore germination, the plants themselves collect still more as they increase in size and in this manner sizeable colonies are built up. Whether *Rhacomitrium* or *Andreaea* first occupies an area seems somewhat a matter of chance, although, in general, the moister areas support *Andreaea*, while *Rhacomitrium* is more abundant in the drier places. In a few cases they grow intermixed and neither seems to crowd out the other.

Beginning of Mat Formation

The occupation of the rock by these pioneers evidently takes place over a long period of time since they grow very slowly and do not spread rapidly. Soil consequently collects at a proportionally slow rate which is still further retarded by the periodic washing rains. When a patch of either *Rhacomitrium* or *Andreaea* attains sufficient size and thickness to retain enough soil or organic matter, it is invaded by either of two lichens or in some cases both. These are *Cladonia subcariosa* Nyl. (fig. 4) and *Cladonia coccifera* (L.) Willd., which mark the beginning of definite mats. These lichens grow on and between the moss plants wherever bits of soil and organic matter have collected, finally almost completely crowding out the moss. A well-developed patch of the invading lichen will show only occasional moss plants persisting. In areas in which *Rhacomitrium* and *Andreaea* are growing intermixed, the two cladonias invade both and a complex mixture of the four results. Mats containing *Cladonia coccifera* are by far more common than those with *C. subcariosa*, the latter seldom occurring alone, while many patches of both *Rhacomitrium* and *Andreaea* were observed in which *C. coccifera* was invading and crowding out the moss. It is not uncommon, however, to observe both *C. coccifera* and *C. subcariosa* invading the same moss clump. Invasion by the lichen usually occurs in the center of the patch of moss where soil and

organic accumulation is greatest and spreads in all directions as the mat is gradually built up.

Cooper ('13) found that *Racomitrium canescens ericoides* (Web.) Schimp. was the pioneer moss upon which cladonias later became superimposed, there being three species of importance, *C. rangiferina* (L.) Web., *C. sylvatica* (L.) Hoffm., and *C. alpestris* L. He likewise described central mat formation spreading in a circular manner.

Occasionally clumps of *Racomitrium* are mixed with *Hedwigia ciliata* Hedw., although the latter seldom reaches any great degree of development, and in a few mats in which some soil has collected *Dicranum scoparium* Hedw. invades the periphery. Although the pioneer mosses are regularly invaded by the two species of cladonia mentioned above, other species may come in at random, particularly on mats with a large amount of organic matter as well as on twigs, sticks, and other debris which happen to lodge in the mat. Among these are *Cladonia fimbriata* (L.) Fries, *C. furcata* (Huds.) Schrad., *C. coniocraea* (Floerke) Spreng., *C. strepsilis* (Ach.) Vainio and *Parmelia molliuscula* Ach. Any of these species which happen to invade the mat aid in the further collection of soil and debris, furnishing bulk and perhaps increasing the water-holding capacity of the mat thus facilitating occupation by other species. Decaying wood and vegetable matter often furnish suitable habitats for *Cladonia caespiticia* (Pers.) Floerke and *C. floerkeana* (Frk.) Floerke var. *intermedia* Hepp., which also increase the general bulk of the mat, and frequently, at this stage, *Polytrichum ohioense* R. & C. was found growing around the edges.

Mature Mats

As soon as *Cladonia coccifera* or *C. subcariosa* gains sufficient hold on the moss mats, the patch increases in thickness by additional invasion of the species of *Cladonia* described above and thus the collection of soil and other materials is greatly increased. When this development has progressed for some time *Selaginella tortipila* A. Br. or either of three larger cladonias, *C. rangiferina* (L.) Web., *C. tenuis* (Flk.) Harm., or *C. mitis* Sandst., may appear. Mixed clumps of all may, in rare cases, appear simultaneously. If *Selaginella* invades first it may occupy the mat to the complete exclusion of the other species for a time. Then usually *C. rangiferina* makes its appearance, growing in with *Selaginella* until there is a mixture of the two or finally it may eliminate the club moss from the central area entirely (fig. 5). Mats with a dense growth of either or a mixture of *C. rangiferina*, *C. tenuis*, or *C. mitis* in the center, surrounded in successive rings by *Selaginella tortipila*, *Cladonia coccifera* or *C. subcariosa*, and either *Racomitrium* or *Andreaea* are common. If *C. rangiferina* precedes *Selaginella* on the mat it may occupy it exclusively and large mats often develop in which *Selaginella* never appears. This is especially true of luxuriant *Racomitrium-C. coccifera* mats in which there are relatively large amounts of soil and organic matter.

The history or stages of development of most mats can be determined by dissecting them and even in extremely large mats bits of the original pioneer moss can be detected as well as successive invaders. Consequently the order of invasion by *Selaginella* and the later cladonias can be determined in this manner. Other mats are seen in which *Selaginella* and *C. rangiferina*, *C. tenuis*, or *C. mitis* appear at about the same time, in which case it may be assumed that the lichens eventually crowd out the former or at least dominate it in somewhat the same manner as when *Selaginella* appears first. Mixtures of the three larger species of *Cladonia* are common and extensive mats four to six feet in diameter are prevalent.

A large number of mats in this stage of development are present scattered over the area, and subsequent growth and increase in size is assumed to be extremely slow. Both *Selaginella* and *Cladonia* as well as the other pioneers are capable of withstanding extreme drought as evidenced by their common habitat in dry exposed regions so that mat formation up to this point is not influenced so much by moisture. With the later invasion by the higher plants which are less drought resistant, however, further development is certainly influenced greatly by the amount of water present. This is shown by comparing mats on dry areas with mats directly beneath seepage lines from the adjoining forest. The mats in the moister places show the presence of higher plants much sooner than those in more desiccated places and for the same reason the latter become much more extensive before they are invaded by these plants. Extensive *Selaginella-Cladonia* mats are scattered over the dry portions of the cliff without supporting any abundance of herbaceous or woody plants. If conditions at any time become favorable for herbaceous plants they may appear and grow for a time only to be killed off by a period of drought, while the pioneer species can withstand such periods and continue to grow and increase the size and general bulk of the mat. In the steeper places, mats not securely anchored increase in weight to the point of toppling down the incline and collecting at the foot of the cliff. Mats in all stages of development can be found here although some of these which are dislodged stop in depressions or behind more secure mats, but it is uncertain whether they continue development. One or two mats were observed in which decay had already begun and superimposed upon both *Selaginella* and *Cladonia rangiferina* were forms of *Cladonia pyxidata* (L.) Hoffm. var. *neglecta* (Floerke) Vanio.

Mats spread in somewhat the same manner as they are built up, with the pioneer mosses spreading out over the bare rock, *Cladonia coccifera* or *C. subcariosa* pushing out over the moss, and *Cladonia rangiferina*, *C. tenuis*, or *C. mitis* and *Selaginella tortipila* in turn invading. This gives the developing mat a decided concentric appearance as has already been noted. Although nearly all of the mats develop in about the same sequence as outlined, certain isolated cases were observed which deviated from this general course of development. In one instance plants of *Cladonia rangiferina* were invading

Racomitrium directly and apparently were spreading. This appears to be rare. Around the edges of the large forested areas occasional plants of *Saxifraga leucanthemifolia* come in directly on *Racomitrium*, but this condition is unusual as is a similar case in which the moss, *Sematophyllum carolinianum* (C.M.) E.G.B., growing in a very moist area was spreading directly on the bare rock followed in turn by *Selaginella tortipila*.

Between the complex *Selaginella-Cladonia* mats mosses and other lichens were distributed throughout the area. These species no doubt play a part in the vegetational development on the rock by retaining a certain amount of soil and organic matter, although they do not aid directly in mat formation. Quite an area is occupied by rather coarse growths of two species of *Umbilicaria*, *U. dillenii* Tuck. and *U. pustulata* (L.) Hoffm. var. *papulosa* Tuck., both of which exclude other species and thus actually hinder mat formation. Isolated patches of *Hedwigia ciliata* appear scattered over the area and the lichen, *Physcia tribacea* (Ach.) Nyl. grows in crevices throughout. In the more scantily vegetated areas both *Parmelia molliuscula* Ach. and *P. conspersa* Ach. are rather commonly present. Any one of the species may eventually collect sufficient soil or debris to favor invasion by either *Cladonia coccifera* or *C. subcariosa* in which case further development proceeds in the manner already described. There are so few of these cases, however, that they are relatively unimportant in the formation of the larger mats.

Herbaceous Invaders

As would be expected, soil collects most rapidly on the upper side of the mat, which, after a time becomes sufficient for certain other species of mosses to come in. Among such mosses are *Polytrichum ohioense*, *Dicranum scoparium*, *Thuidium delicatulum* Mitt., and occasionally tufts of *Leucobryum glaucum* Schimp. These additional plants greatly facilitate the collection of soil and as accumulation continues *Saxifraga leucanthemifolia* Michx. appears around the outer edges especially of the moister mats (fig. 7). On the mat proper, either separately or together, the grasses, *Danthonia spicata* (L.) Beauv. and *Panicum huachucae* Ashe, establish themselves (fig. 6). *Cynthia montana* (Michx.) Standley sometimes appears with the grasses. On some of the larger clumps *Carex* sp. may occur and in two places *Dryopteris marginalis* (L.) A. Gray (fig. 8) had gained a foothold but was not thriving.

When a mat has persisted for some time it is invariably made up of a series of girdles each migrating in a centrifugal direction encroaching on its neighboring species. On a flat rock this spreading or enlargement results in a more or less concentric arrangement but on this steep slope the protection afforded by the mat facilitates the growth of pioneers on the lower side and the spread is consequently mostly downward forming an oval. Two factors contribute to the eccentric form of the mats, namely, the physical protection against erosion and the supply of moisture which is extended over several

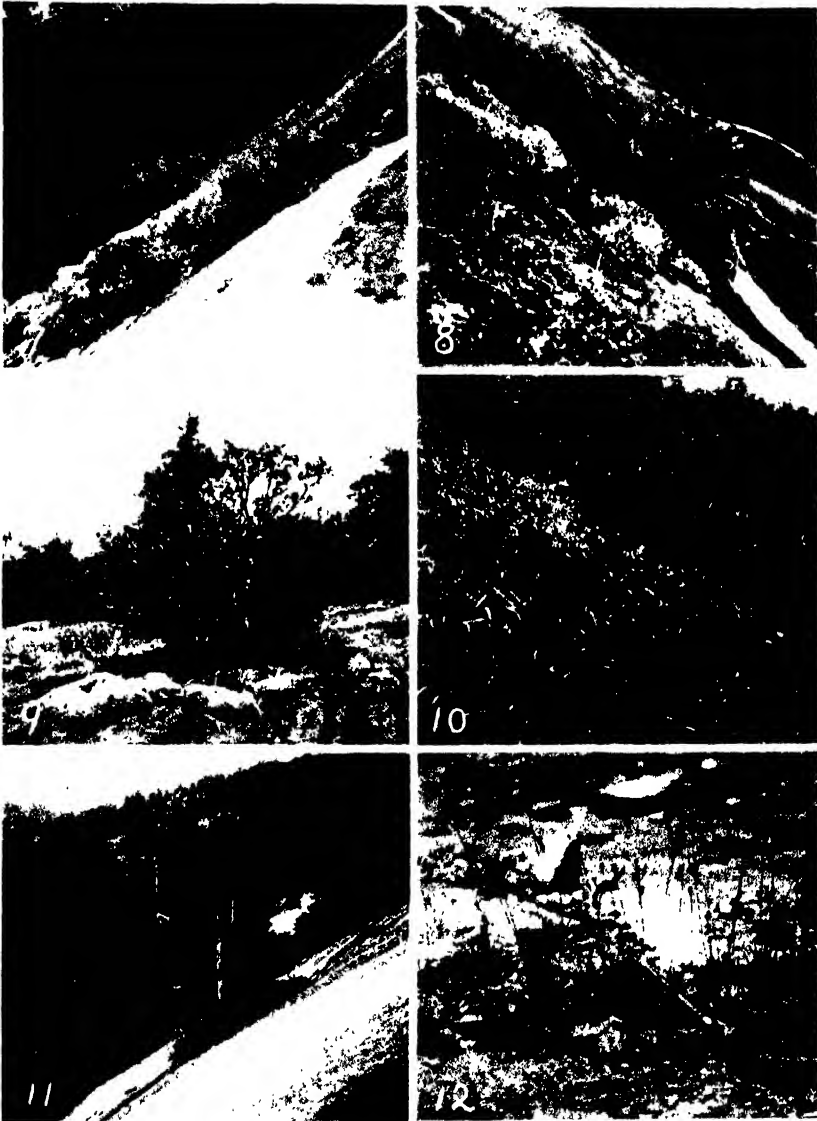


FIG. 7. One of the moister mats with *Saxifraga leucanthemifolia* around the margin.

FIG. 8. An older mat, anchored behind a log, which supports *Danthonia spicata*, *Carex* sp. and *Dryopteris marginalis*.

FIG. 9. *Chionanthus virginicus* the first woody species to establish itself.

FIG. 10. An opening in the forest where *Panicum virgatum* is dominant and *Chionanthus* is making a scattered appearance.

FIG. 11. *Juniperus virginiana* appearing. The low material on the upper side of the mat is mainly *Diervilla sessilifolia*.

FIG. 12. *Talinum teretifolium* growing on a bare ledge. (Note pencil.)

days as it gradually seeps from the lower edge. This seepage from the larger mats continues for days after a rain and, where this occurs, the lower margin instead of having the characteristic bare rock pioneers will be fringed with a strong development of *Sphagnum capillaceum* (Weiss) Schrank, *Thuidium delicatulum*, *Campylium chrysophyllum* (Brid.) Bryhn., *Hypnum imponens* Hedw., and an abundance of *Saxifraga leucanthemifolia*.

Woody Invaders

When a mat has built up to a depth of several inches the first woody species, *Chionanthus virginica* L. (fig. 9), makes its appearance and somewhat later seedlings of *Acer rubrum* L. commonly gain a foothold. All the woody plants which start do not survive and those which survive grow slowly. This is particularly true of *Juniperus virginiana* L. (fig. 11) which often germinates but rarely lives to reach any size. One red maple, ten feet tall, was over 25 years of age; fringe trees 1.5 to 2 inches in diameter were often 40 years old. Unless the woody species find anchorage in crevices, which are rare, the mats are still not permanent, and even with strong herb development the roots are imbedded only in a mat which can be raised at the margin and rolled like a heavy rug. As a consequence even the larger mats supporting woody plants sometimes slide to the bottom in a jumbled mass. If such a falling mass strikes a more stable or better anchored mat it may lodge there and, if the whole mass holds, add to and speed up the vegetational development on that area. When large or small tree trunks slide down from above and are miraculously checked somewhere on the slope a new mat rapidly forms above them. Several of the larger mats are anchored behind windfalls.

The mats in which *Chionanthus* and *Acer* occur that have been established for some time are relatively stable and tend to maintain their condition indefinitely. A transect from the lower to the upper margin of one of the more stable, older mats shows the complete successional series from *Andraea* and *Racomitrium*. On the grassy mat *Lilium superbum* L. is characteristically present and *Cynthia montana* not infrequent. Above the trees *Diervilla sessilifolia* Buckl. (fig. 11) forms a narrow zone fringed with *Pycnanthemum dubium* A. Gray.

Forest on Old Mats

Two of the vegetated areas are much more extensive than any others. These are characterized by a more varied woody flora and are the oldest mats present. Neither mat is isolated since both extend down over the rock as tongues from the forest above. The woody species consequently grade from those of the hardwood forest above to *Acer* and *Chionanthus* near the lower margin. Between are species which are seemingly indicative of the trend of development of any of the mats if they could progress without interruption. The dominant tree species are *Tsuga canadensis* (L.) Carr., *Juniperus virginiana* L. and *Pinus strobus* L., all of which are undersized and have grown

very slowly. Borings showed a hemlock 2 inches DBH to be 48 years old; a juniper 4 inches DBH, 58 years; white pine 3 inches DBH, 42 years. The trees highest on the mat and nearest the hardwoods have obviously made better growth than those lower down the slope for near the top an 8 inch hemlock was only 61 years old.

The understory on these larger mats is made up of reproduction in all sizes of the above species and, locally, well developed clumps of *Rhododendron catawbiense* Michx. and *Kalmia latifolia* L. Neither of these was more than four to five feet tall and borings, difficult to obtain because older branches are much decayed, showed their ages to be well over 40 years. Other shrubs present include *Aronia melanocarpa* (Michx.) Britton, *Vaccinium arboreum* Marsh, and *Gaylussacia baccata* (Wang.) C. Koch. The floor covering was composed of *Hypnum imponens* Hedw., *Polytrichum ohioense*, *Leucobryum glaucum*, *Tetraphis pellucida* Hedw. (*Georgia pellucida* Rabenh.), *Pohlia nutans* Hedw., *Sphagnum compactum* DC., *Cladonia squamosa* (Scop.) Hoffm., and *C. strepsilis*.

Increment borings of the trees showed marked irregularities in rates of growth at different periods in the past. Comparison of numerous borings revealed that these irregularities were the same in different individuals. All of the species began growth at a very slow rate and this was followed by a period of uniform growth with slightly larger rings. Regardless of age the annual increment was suddenly much reduced about 23 to 25 years ago and very poor growth followed until 12 years ago when all species showed a marked increase in annual growth that continued to the present. This trend was apparent in hemlock and red cedar regardless of age or size and to a lesser extent in white pine. The trees bored ranged from 40 to 60 years of age and from 2 to 8 inches in diameter. Comparison of actual ring widths was not practical because some trees grew much better than others. Measurements for a 58 year red cedar, 4 inches in diameter, illustrate the general trend for all species: first 15 years, 0.25 inch; next 18 years, 0.75 inch; then 13 years, 0.25 inch; and the past 12 years, 0.75 inch.

The early slow growth can be explained as due to competition under overtopping species or possibly the mat was much more open and exposed at the time with attendant poor moisture conditions. That this should be followed by a rather extended period of uniform growth when the individual had established itself might reasonably be expected. What caused the abrupt decrease in growth 25 years ago is, however, highly problematical. Several large, partially decayed, stumps may possibly explain the rapid growth initiated 12 years ago. The stumps do not appear as though they had been cut and the presence of several partially decayed logs at the base of the cliff and suspended on different mats would indicate that they may be windfalls. The increased moisture made available by the elimination of these larger trees might well have been the factor which stimulated the more rapid growth of the survivors.

Woody species on the larger mats, beside the conifers and shrubs mentioned, include *Quercus montana* Willd., *Q. coccinea* Muench., *Prunus serotina* Ehrh., *Rubus* spp., *Amelanchier* sp. and rarely a stunted hickory. An ash of which all individuals present were small appears to be *Fraxinus biltmoreana* Beadle. Around the margins several herbs, not previously discussed, are characteristic. These include *Coreopsis major* Walt., *Kneiffia tetragona* (Roth.) Pennell, *Lysimachia quadrifolia* L., *Uvularia sessilifolia* L., *Polygonatum biflorum* (Walt.) Ell., *Smilacina racemosa* (L.) Desf., *Aralia nudicaulis* L. and *Dryopteris marginalis* (L.) A. Gray. The outer fringe, in addition to coarse growths of *Scelaginella tortipila*, *Cladonia rangiferina*, *C. tenuis*, and *C. mitis*, contains *Sphagnum capillaceum*, *Sematophyllum carolinianum*, *Aulacomnium palustre* Schwaegr., *Hypnum molluscum* Hedw., *H. imponens*, *H. crista-castrensis* Hedw., *Thuidium delicatulum*, *Eurhynchium serrulatum* (Hedw.) Kindb., *Plagiothecium striatellum* (Brid.) Lindb., *Leucobryum glaucum*, *Cladonia incrassata* Floerke, *Peltigera rufescens* (Weis.) Humb., and *Cladonia pyxidata neglecta*.

THE SURROUNDING FOREST

The forest surrounding the cliff is predominantly oak-chestnut. Several of the chestnut trees (*Castanea dentata* (Marsh.) Borkh.) on the lower slopes appear untouched by blight but on the ridges almost all are dead. The most important oaks in the order of their apparent abundance are *Q. montana*, *Q. borealis maxima* (Marshall) Ashe., *Q. alba* L., *Q. coccinea*, and *Q. velutina* Lam. Less important trees are *Acer saccharum* Marsh., *Liriodendron tulipifera* L., *Fraxinus biltmoreana* Ashe., and an occasional hickory. The understory and shrubs include *Juniperus virginiana* L., *Cornus florida* L., *Aesculus octandra* Marsh., *Chionanthus virginica* L., *Asalea calendulacea* Michx., *Kalmia latifolia* L., and *Rhododendron catawbiense* Michx. The trees are uneven aged and vary considerably in size. Some are three feet in diameter and exceed 300 years in age. The forest at the top of the ridge appears younger but the rate of growth is apparently much slower for the average large oaks which were 20 to 25 inches in diameter, were 300 to 350 years of age. The habitat becomes drier and the soil, due to erosion, is not as deep. Here chestnut oak is less abundant and white and black oak relatively more important. Numerous dead chestnuts are scattered throughout, and hickory forms a strong understory in the drier parts.

As seen from a distance the woods seem to cover the surrounding slopes fairly uniformly even though the bluffs appear as steep as the bare area. Closer observation, however, discloses that the wooded slopes have rough and irregular surfaces, the manner of weathering having resulted in numerous broad, outcropping ledges and many crevices of all sizes. Herein lies the explanation of the bare and forested bluffs. The ledges and crevices prevent wholesale denudations when mats are released and soil is retained in some quantity wherever it accumulates at all. Then, the woody plants which be-

come established, their roots anchored in the crevices, bind themselves and the soil firmly to the face of the cliff. The smooth rock faces, retaining scarcely any soil and fairly few crevices in which trees and shrubs may become anchored, remain indefinitely in a semibarren state conditioned by the rate and amount of soil accumulation.

On the forested bluff small rock areas frequently outcropped which had all the stages of succession characteristic of the larger areas. With one exception where *Talinum teretifolium* Pursh. (fig. 12) was thriving and nothing else, these small areas were too small or too steep for soil to accumulate in quantity. The rate and amount of soil accumulation can be satisfactorily used to explain the nature and development of the vegetation on the entire bluff.

SUMMARY

The vegetation of and surrounding a barefaced cliff in the mountains of western North Carolina is described. Stages in development were observed from bare rock pioneers, to woody species.

Bare rock pioneers are *Rhacomitrium heterostichum* var. *ramulosum* or *Andreaea rupestris*, from either of which complex mats are built up through the successive invasion of either *Cladonia coccifera* or *C. subcariosa*, *Selaginella tortipila*, and any or all of *C. rangiferina*, *C. tenuis*, or *C. mitis*, with anomalous species of mosses and lichens intermingled. Invasion by higher plants is initiated by *Saxifraga leucanthemifolia*, followed by either *Danthonia spicata* or *Panicum huachucae* or both. Mats spread centrifugally in the same order.

Mats reaching sufficient size are invaded by woody plants such as *Chionanthus virginica*, *Acer rubrum*, and *Juniperus virginiana* and still larger mats are dominated by *Tsuga canadensis*, *Juniperus virginiana*, and *Pinus strobus*. The understory is composed of reproduction of these species as well as *Rhododendron catawbiense*, *Kalmia latifolia*, *Aronia melanocarpa*, *Vaccinium arboreum*, and *Gaylussacia baccata*.

The surrounding forest is predominantly oak-chestnut including *Q. montana*, *Q. borealis maxima*, *Q. alba*, *Q. coccinea*, *Q. velutina*, and *Castanea dentata* (mostly dead). With the above were associated *Acer saccharum*, *Liriodendron tulipifera*, *Fraxinus biltmoreana*, and an occasional hickory. The understory and shrubs included *Juniperus virginiana*, *Cornus florida*, *Aesculus octandra*, *Chionanthus virginica*, *Azalea calendulacea*, *Kalmia latifolia*, *Rhododendron catawbiense*.

Mat formation accompanied by soil accumulation and consequently all stages of succession are influenced by the presence of crevices in the rock combined with the steepness of the slope. Moisture may at times become an important factor in local areas. In general it is concluded that the amount and rate of soil accumulation determines the nature of the vegetation on the entire bluff.

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REVIEWS

TERTIARY AND MODERN FLORA OF IDAHO ¹

Bringing together exact lists of the plants in his fossil beds and detailed, almost sociologic lists of the flora now living in adjacent regions, Dorf has presented a striking picture of the likeness of the vegetation of long ago to that of the present. The Weiser beds are believed to be uppermost Miocene or lowermost Pliocene, with a preference for the latter. "The flora is composed entirely of typically temperate genera, the majority of which are still living in Western North America. Out of a total of 35 species which show striking similarities in leaf or seed characters to modern species, 68.5 per cent are comparable to species now living west of the Great Plains and 42.8 per cent are comparable to species at present restricted to the Pacific states." ". . . the Weiser flora is essentially similar to the *Lithocarpus-Quercus-Arbutus* community and its associated communities of the inner Coast Ranges of California. These communities grow at present on the inner, less mesic borders of the redwood forest and are dominated by species whose fossil equivalents are likewise the dominants of the Weiser flora. The inferred climatic requirements of the Weiser flora are mild temperatures, dry summers, and an annual rainfall of between 20 and 30 inches. These conditions are in contrast to the more humid climates inferred for the earlier Miocene floras of the same general region, and to the cooler and more arid conditions which prevail in the region today."

H. S. CONARD

GRINNELL COLLEGE, GRINNELL, IOWA

A SWISS FLORA ¹

There has just been completed an elaborate and detailed flora of southeastern Switzerland by two outstanding ecologists. The mountainous region covered by this flora has an annual precipitation of 90 to 150 cm. in the north and slightly more in the south. The growing season varies much with altitude. Three regional divisions are recognized; a northern, a central, and a southern whose valleys and montane slopes are characterized by forests of beech, of pine and larch, and of mixed oak, linden and beech respectively. The subalpine and alpine portions of these three regions are subdivided ac-

¹ Dorf, E. 1936. A late Tertiary Flora from southwestern Idaho. Contributions to Palaeontology. *Carn. Inst. Wash. Publ.* 416, 73-124. 3 pl., 29 fig.

¹ Braun-Blanquet, J. und Eduard Rübel. 1932-1936. Flora von Graubünden. *Veröff. Gebot. Inst. Rübel in Zürich* 7 (1-4): pp. 1-1695. Map. *Hans Huber, Bern and Berlin. Fr.* 90.

cording to the various mountain areas. Special attention is given to the ecological and altitudinal limitations of the various species.

The arrangement and nomenclature follows those in the *Flora der Schweiz* by Schinz and Keller. In the first *lieferung*, which appeared in 1932, there is an extensive bibliography and a vegetation map.

The work is one of the first floras to give the adequate ecological setting of each and every species and it will be indispensable to all students of alpine vegetation.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

EXPERIMENTAL PLANT PHYSIOLOGY

The fact that all ecology has or should have a physiological basis makes a recent book by Loomis and Shull¹ most welcome to plant ecologists. It is essentially a description of a series of experiments and laboratory exercises designed to familiarize the student with the principles and problems of plant life, to teach him to observe and record accurately, to recognize causes and effects and to be distrustful of unsupported statements. The experiments are divided into a more elementary and a more advanced group and in each group are arranged according to subject matter. A glance at some of the chapter headings will give some idea of the topics included. Among those of more immediate interest to ecologists are: Physical measurements; Measurement and control of plant environment; and Statistical methods. Other chapters that touch ecological fields more or less directly are entitled: Water relations of plants; Transpiration; Photosynthesis; Plant pigments; and Growth and movement. In addition there are several chapters on various phases of biochemistry.

There are numerous citations of literature brought down to 1935 and appearing as footnotes. Special attention seems to have been given to recent contributions by American workers. The chapter on statistical methods, contributed by G. W. Snedecor, contains a clear and comparatively non-technical description of the methods of statistical analysis most in use by biological workers. It would be of great service to ecologists with little or no training in higher mathematics.

Not the least important part of the volume is an appendix which contains the tables that are required for the experiments in the main part of the book. There are 33 such tables of constants ranging from those of atomic weights of elements, of conversion of U. S. weights and measures to metric, of relative humidity determinations, of specific heats, and of density of mixtures of alcohol and water, to the values of various statistical units.

¹ Loomis, Walter E. and Charles A. Shull. 1937. *Methods in plant physiology. A laboratory manual and research handbook.* xviii + 472 pp. 93 fig. *McGraw-Hill Book Company, New York.* \$4.50.

The brief but significant discussion of the principles involved, the clear and concise description of the experiments and the thoughtful questions following each experiment add to the value of the book. The wide experience and high reputation of the authors together with the excellent work of the publishers combine in making this a valuable contribution to experimental plant science which will be welcomed alike by physiologists and ecologists.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

J. ARTHUR HARRIS, BOTANIST AND BIOMETRICIAN ¹

Ecology, like other branches of knowledge, has been represented in its several phases by notable scientists. Of recent years, the outstanding ecologist-biometrician has been J. Arthur Harris who, from 1924 until his sudden death in 1930, was head of the department of botany at the University of Minnesota, coming to this post after 18 years with the Carnegie Institution. The book, a memorial to Harris and his latest scientific labors is in three parts: (1) Harris, the Man by R. A. Gortner; (2) Harris, the Botanist by C. O. Rosendahl; and (3) Harris, the Biometrician by A. E. Treloar. Interspersed are several posthumous papers finished by his students.

Gortner, a lifelong friend (and, in the best sense, hero-worshipper) of Harris, lends a human touch to his treatise by presenting Harris's most idealistic writing, a poem "To Pahvant" and his two most humorous ones, a metrical pseudo-lament on "Desert Beef," and an after-dinner sarcasm in "A great institute for the study of the psychology of the mule."

As the ancient mariner held the bridegroom, this book held me, so truly did it reflect my friend and teacher. J. Arthur Harris is still among us who are his scientific offspring, principally as an inspiration to "follow through" on the trail he blazed. To us, and to others we hope, this small volume is a lease to live again, for a brief spell, a day flooded with the scientific leadership that radiated from his presence; an hour beside the campfire or around the evening table when he helped us by story and jest to become men; a minute, when at a desert shrine, we saw him lifted up in spirit. This minute we love, and we love too his poem "To Pahvant" which we heard first only after his death.

TO PAHVANT

To the unthinking traveler,
A roughly rounded butte,
A landmark, merely, in the wastes
Of drifting sand and whitened clay,
And blighted growth of spiny things.

* * * * *

¹ Rosendahl, C. O., R. A. Gortner, and G. O. Burr. 1936. J. Arthur Harris, botanist and biometrician, 209 pp., 43 figs. *The University of Minnesota Press, Minneapolis*. \$2.50.

Lone landmark of the burning wastes!
Faint record of a wondrous past!

* * * * *

To me you are a sacred shrine
Where, in the desert's vast expanse,
I can forget the pettiness
And poverty of soul of those
Who, seeing, fail to understand.

I see him now—hat off and eyes aglow; for the moment work pauses and jesting is aside. We wait at the edge of the old volcanic cone, while Dr. Harris picks his way among sharpened rocks and over crooked cranny to a somewhat elevated table of lava rock. With the low western sun burning the horizon as though “of skies lit red by lurid flames,” for perhaps 20 minutes he stands reverentially still. Then he comes quietly back; without a word we follow him slowly down the butte. No one speaks; no one needs to; all know he stood at Sinai.

Every summer for 10 years he collected leaves of desert plants in the desiccated Bonneville Lake bottom which is now the Sevier desert of western Utah. His project was a monograph on plant geography that could be superimposed on Gilbert's geological classic of the glacial Lake Bonneville—wave-cut terraces on the hillsides; bars of assorted gravel and sand in the coves; and endless stretches of salt shrub where deep water on evaporation left salt on the surface in some places and in others, buried with the soil. Centuries of snow and rain, of soil leaching and sand blowing, incorporated the salt with the soil and prepared, in the space of a few miles, a cross-section of plant life from salt desert flat at 4,400 feet elevation with 6 or 7 inches of precipitation, across the series of gravel shore lines that rise some 800 feet and have 12 to 20 inches precipitation, on up the slopes to the mountain crest at 10,200 feet where the rainfall is 30 inches. Here Nature left the marks of a geological drama that Gilbert first read and a fantasy in plant life that Harris was the first to see. Of course, we all see it now, just as the courtiers could stand the egg on end after Columbus showed them how.

Of his 300 printed papers this was to be the classic—the phytogeography of the Bonneville basin. The study was based on sap properties, as measured by total concentration and electrical conductivity, of plants collected in a series of sites between salt flat and mountain top. At the back of his mind was a never-fully-explained principle of evolutionary plant relations. At last he felt the field work completed and began to marshal up the data. Then he was gone.

In the treatment of Harris the Biometrician, Treloar gives the history of Harris's interest in statistical analysis and something of his contribution.

Following this chapter are five papers involving statistical studies, largely of human birth and fecundity, one of which is on statistical methods: "The distribution of errors of analysis." These papers illustrate the wide application of the statistical method to biological problems, a field in which Harris led for more than twenty years.

In the section of Harris the Botanist, his accomplishments and attitude are treated by Rosendahl, who displays a sympathetic insight into Harris's high qualities. He points out how Harris gradually turned from the statistical testing of Darwinism to a study of the physiological and chemical aspects of plant phenomena in Jamaica, Hawaii, Florida and finally in the Great Basin, whence he had at the time of his death an immense accumulation of field data. These raw data in the botanical field have already appeared in print.²

The present book carries also a major ecological contribution in a joint paper by Dr. Harris and one of his students, Vernon A. Young, now at Syracuse University: "Some chemical factors of the soil that influence the distribution of desert vegetation." It is principally a study of the soil-salt relations of sagebrush (*Artemisia tridentata*) and of greasewood (*Sarcobatus vermiculatus*). Thirteen habitats of pure sagebrush, pure greasewood, and mixed sagebrush-greasewood were studied in Juab, Pahvant, Ferner, and Tintic valleys (central western Utah) on the Bonneville Lake bed and three habitats lying outside the lake bed but within the drainage basin.

Pure greasewood as compared with pure sagebrush habitats show on the average a great accumulation of chlorides and carbonates and a distinctly greater electrical conductivity. Alkalinity rather than salinity of the soils under greasewood and sagebrush was found to be the important determining factor in the distribution of these two plants. This is especially clear on the mixed sagebrush-greasewood habitats where salt content of soils under sagebrush increased as that of greasewood soils increased. Alkalinity was shown to decrease with depth, a result of upward leaching by evaporation. In this mixed vegetative type immense soil heterogeneity in small spots was also manifest. Roots of sagebrush and greasewood plants occupied immediately adjacent square yards of soil that practically always differed sharply in alkalinity. This soil heterogeneity was so definite and the unit areas so small that soil samples had to be drawn by putting the auger down among the branches and roots of a given plant. A hole at the edge of the bush in many cases was in another edaphic habitat. These points are expressed in the summary statements as follows:

"4. Alkalinity rather than salinity is an important determining factor in the distribution of greasewood and sagebrush. High alkalinity is distinctly favorable to the former and unfavorable to the latter.

² Harris, J. Arthur. 1934. The physico-chemical properties of plant saps in relation to phytogeography: data on native vegetation in its natural environment. *University of Minnesota Press*, 339 pp.

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PROCEEDINGS

BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT ATLANTIC CITY, NEW JERSEY, DECEMBER 29, 1936, AND JANUARY 1, 1937

Meeting of December 29, 1936

The Society met at the Ambassador Hotel at 9 A.M., Vice-President James G. Needham presiding.

The Vice-President appointed a nominating committee consisting of: Walter P. Taylor (chairman), W. C. Allee, and G. D. Fuller.

There being no further business to transact, the meeting adjourned at 9:30 A.M.

Meeting of December 31, 1936

The Society met at the Ambassador Hotel at 9 A.M., Vice-President Needham presiding, and twenty-eight members present. Reports of officers and committees were first called for.

REPORT OF THE SECRETARY-TREASURER

January 2, 1936, to December 18, 1936

Receipts

Received from A. G. Vestal, retiring secretary	\$ 472.09
Dues from members	2,557.30
Royalty, Naturalists' Guide	8.10
	\$3,037.49

Disbursements

Printing	
Bulletin (March, June, October, December)	\$ 165.43
Other printing	59.75
Subscriptions	
Ecology, payments for members	1,476.00
Ecological Monographs	335.00
Secretary's expenses	
St. Louis meetings	16.39
Madison conference	8.00
Atlantic City meetings	85.00
Postage, telegrams, supplies	135.11
Clerical help	33.00
Committee expenses	
V. E. Shelford	59.68
H. de Forest	15.20

W. F. Loehwing	5.00
Bank charges, exchange	13.61
<i>Total disbursements</i>	<u>\$2,407.17</u>
<i>Balance on hand</i>	<u>630.32</u>
	<u>\$3,037.49</u>

Examined and found correct December 18, 1936.

L. S. WALLEN,
Auditor

REPORT ON MEMBERSHIP, 1936

Total membership as of January 1, 1936	671	
Active	539	
Sustaining	81	
Associate	40	
Life	11	
Additions to membership as of December 31, 1936	75	746
Active	62	
Sustaining	5	
Institutional	4	
Associate	4	
Losses during 1936		69
Deceased	6	
Cancellations	3	
Lapsed	60	
Grand Total, Paid-up members	677	
Potential total membership	737	

Respectfully submitted,

ORLANDO PARK, *Secretary-Treasurer*

The report of the Secretary-Treasurer on motion duly seconded was accepted.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY FOR THE FISCAL YEAR, DECEMBER 1, 1935–NOVEMBER 30, 1936

Receipts

Cash on Hand (Statement of 1935)	\$1,229.22	
Dr. Arthur G. Vestal, Treasurer, E. S. A. }		
Dr. Orlando Park, Treasurer, E. S. A. }		
34 memberships 1935 at \$3.00	\$ 102.00	
533 memberships 1936 at \$3.00	1,599.00	
121 memberships 1937 at \$3.00	363.00	2,064.00
Subscriptions: 1936	1,469.88	
1937	316.30	
1938	3.75	1,789.93

Advertising	94.00	
Single numbers and back volumes	236.29	
Authors' payments		
J. E. Weaver	98.79	
Authors' excess pages		
National Geographic Society for Robert F. Griggs ...	100.00	
J. E. Weaver	50.00	
F. W. Albertson	75.00	225.00
<hr/>		
Transportation of set of <i>Ecology</i> shipped		
To Utah Agricultural College	4.08	
Reprints		
Dolores M. Bullock	12.50	
Dr. T. D. Mallery	10.00	
Dr. Lewis M. Turner	10.00	32.50
<hr/>		<hr/>
		\$5,773.81

*Disbursements**Printing*

Lancaster Press, Inc.

January issue and reprints	\$1,020.48
April issue and reprints	897.79
July issue and reprints	1,152.57
October issue and reprints	956.98
	<hr/>
	\$4,027.82

George Banta Publishing Co.

250 copies of January issue reprinted	362.87	\$4,390.69
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Illustrating

Revere Photo Engraving Co.	347.61	
Ad Plate Engraving Co.	73.09	420.70

<i>Advertising</i>	124.71
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<i>Purchase of Back Volumes</i>	29.72
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Office Expenses

Business:

Clerical Assistant for 12 mos. at \$10	120.00
Postage	48.00
Expressage	17.98
Stationery	7.50
Wrapping paper and twine	18.70

Editorial:

George D. Fuller	52.10	
Alfred E. Emerson	25.00	
Robert Gregg	48.00	337.28

Miscellaneous

Refunds on subscriptions	10.40
Refund—Dolores M. Bullock; excess payment	6.12

Audit of books for last fiscal year	5.00	
Collection charges70	22.22
		<hr/>
Balance, November 30, 1936	448.49	\$5,773.81
		<hr/>
Cash in bank	\$323.49	
Checks in hand	\$50	
	75	125.00
	<hr/>	
	\$448.49	
	<hr/>	

Examined and found correct, December 18, 1936.

H. P. SCHOENBERNER,
Auditor

STATEMENT SHOWING ASSETS AND LIABILITIES, NOVEMBER 30, 1936

Assets

Cash in bank	\$323.49	
Checks in hand	125.00	\$448.49
	<hr/>	
<i>Bills Receivable</i>		
Subscriptions: 1935	\$10.00	
1936	4.20	
1937	19.90	34.10
	<hr/>	
Single numbers	2.75	
Advertising	16.00	52.85
	<hr/>	<hr/>
		\$601.34

Liabilities

None

Assets over Liabilities	<u>\$601.34</u>
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Circulation data as per mailing list for the October issue:

	1935	1936
1. Members of the Ecological Society	434	533
2. Subscribers	462	450
3. Exchanges	99	80
4. Advertisers	12	21
5. Editorial Office	2	2
	<hr/>	<hr/>
	1,009	1,086
Number of copies ordered printed per month	1,200	1,400

(signed) C. STUART GAGER,
Business Manager of Ecology

It was moved that the report of the Business Manager be accepted, except for the item regarding the reprint of the January issue; this item to be referred to the incoming Board of Directors for investigation and report to the Society. This motion was seconded and carried.

REPORT OF THE EDITORS OF ECOLOGY

We have been able to publish 714 pages this year as compared with 680 pages last year. This increase is largely owing to funds contributed by authors and institutions for extra pages. A policy concerning the publication of all papers beyond 25 printed pages is being arranged in cooperation with the editors of *Ecological Monographs*.

In general we are able to print papers within 6 to 10 months of their final preparation for publication and delay is often the result of inadequately prepared papers.

The editors wish to take this occasion to thank the members of the Editorial Board for their cooperation during the year.

(Signed) GEORGE D. FULLER,

ALFRED EMERSON,

Joint Editors

The report was accepted.

REPORT OF THE EDITORS OF ECOLOGICAL MONOGRAPHS

On behalf of Dr. R. O. Rivera, Executive Secretary, Duke University Press, and Business Manager of *ECOLOGICAL MONOGRAPHS*, we present the following report for *ECOLOGICAL MONOGRAPHS* for the fiscal year ending June 30, 1936:

<i>Income:</i>		<i>Expense:</i>	
Advertising	\$ 583.75	Advertising	\$ 336.00
Subscriptions	1,236.65	Printing	3,359.93
	<hr/>		<hr/>
	\$1,820.40		\$3,695.93
Deficit	\$1,875.53		

The circulation of the journal is as follows:

Paid subscriptions	213
Duke University Library exchanges	18
Free exchange and complimentary	19
	<hr/>
	250

(Signed) A. S. PEARSE,

C. F. KORSTIAN,

Joint Editors

The report was accepted.

REPORT OF THE COMMITTEE ON PRESERVATION OF NATURAL CONDITIONS

In the first year of the Society's history (1916) there was much discussion of committees, especially research committees. A committee on climatology and a committee on soil temperature were set up. Various schemes for the organization of committees were devised and rejected. This committee on the preservation of research materials was in the background and the chairman was appointed March 17, 1917, by Ellsworth Huntington, second president of the Society, in the following words, "My dear Professor Sheldford:—I am very glad you have taken the initiative in suggesting a committee on The Preservation of Natural Conditions for the Ecological Study. . . . I take pleasure in appointing you chairman of such a committee with power to select your associates . . . five members at present. Apart from any immediate measures having to do with *legislation* would it not be well for the committee to . . . list typical areas which ought to be preserved in various parts of the country?" In getting the list together a series of state representatives were appointed to describe natural areas and enlist the support of local societies in securing their preservation. Previous to 1920 this group was not well organized. Descriptions and list of societies interested in such matters were only partially in the hands of the central committee.

The publication of the materials collected as the "Naturalists' Guide to the Americas" was authorized by the Society at the Toronto meeting in 1921. In the course of the preparation of the descriptive list of natural areas a grant of \$300 was received from the National Research Council (1920–21). This was used to obtain descriptions of suitable areas, to work for their preservation and to secure two representatives in each state and province. These representatives prepared the Naturalists' Guide materials and compiled a list of societies in the various states and provinces and one of the United States Forest Districts.

The grant from the Council sufficed to collect the manuscripts but left nothing for their revision and editing. An application for an additional sum was unfavorably received and hence the book went to press imperfectly prepared. In spite of these difficulties, however, it received a number of good reviews and mentions. It was one of 40 books from the United States selected by the American Library Association for a world list of 600 notable books of the world for 1926.

In 1924 the list of societies and state representatives was so well organized so that when Dr. W. S. Cooper proposed to urge the setting aside of the Glacier Bay as a National Monument, he was able to call on these societies and state representatives to write government officials to set it aside from the public domain. This campaign was said to be one of the strongest demonstrations experienced by the Department of Interior and the Glacier Bay National Monument was established by Presidential proclamation in 1925.

During the period of final preparation and publication of the Naturalists'

Guide several worked together as joint chairmen with Dr. W. G. Waterman as senior chairman from 1926–1929. He did much during that period and the preceding two or three years to establish the state organization. In 1927 he asked the local societies to exert pressure against the Bechler Basis irrigation project which violated Yellowstone Park. The bill was defeated. Dr. Waterman resigned as chairman in 1929.

In 1926, V. E. Shelford, H. C. Oberholser and W. P. Taylor were appointed as a committee to further facilities for continuous observation which might bear on cycles. The reorganization of the committee on the Preservation of Natural Conditions was placed in the hands of this group with V. E. Shelford as chairman. The chairman was asked to complete an organization plan, try it out, and on the basis of experience to present the Society with a plan for a permanent organization and for means of supporting the committees. This would have been presented in 1933 but for the depression and financial reverses of the Society which a little later caused members of the Executive Committee to suggest that the work be discontinued altogether. The suggestion of discontinuation led to the appointment of a committee composed of F. Ramaley, B. C. Tharp, L. R. Dice, and A. H. Wright primarily to decide whether or not it should be continued.

Since the foundation of the Society attempts have been made to perfect organizations in the states and provinces. Dr. Waterman made an especial effort in that direction. To reduce the labor of the central office, regional chairmen who could help with the organization and maintenance of committees in several states were planned but an insufficient number of men willing to undertake the work rendered this impracticable. However, long experience has indicated that three state representatives would be better than two as they would represent more interests. Since the committee has been in operation under the present leadership a strong campaign to stop the appropriations of \$1,300,000 per year for rodent and predatory animal control was put on.

A nature sanctuary plan has been developed and published in *ECOLOGY* 14: 240–245. This idea was adopted by the National Parks Association which devoted a number of publications to it and it was adopted and quoted by the National Park Service in *FAUNA OF THE NATIONAL PARKS* 2: 123–130. Many letters of commendation have been received regarding this publication and several calls for reprints have been received.

Attempts were made (through the appointment of committees) to have institutions of learning cooperate in acquiring areas for field study. Standards of educational qualifications were suggested but nothing was accomplished due to lack of response by members.

Since the Roosevelt administration began its work the Committee on Preservation of Natural Conditions has been in communication with the Beck Committee as a result of which local representatives of the society in several states were urged to set up resettlement, game, and water fowl projects.

A warning was sent to all state representatives to watch CCC camps relative to destruction of natural conditions in state parks and forests.

The attention of F. E. Clements, who has acted as advisor in soil conservation projects, has been repeatedly called to the poor training of men employed and he has been urged to try to influence the administration as much as possible in the direction of improving the training of personnel, and the application of correct ecological principles. The secretary of the Preservation Committee asked the head of the Biological Survey if the Ecological Society could be of any service in helping to save game, recreation, natural areas under the Taylor Grazing Act. He did not indicate that any assistance was needed, but rather the contrary.

In Illinois the local committee selected six areas, cruised two of them in midwinter, and repeatedly (five times) refiled reports on them as bureaus changed. A protest was sent to the State Conservation Department relative to permitting the use of thallium to poison crows.

REPORT FOR 1936

The resolutions concerning CCC camps were forwarded to the proper authorities (see report for 1935). Conrad L. Wirth, National Park Service, asked for details about the violation of natural areas by CCC workers. He was informed of the sources of the objections, that near the New England cities many natural areas have been seriously disturbed and rendered too accessible to automobile drivers, and that in Iowa certain grassland areas have been cut up by roads. Attention was also called to the girdling of all beech trees in the Union County, Illinois State Forest. The results of this could not be felt in the improvement of other hard woods for 200 years, meanwhile, the most important nut crop for game animals has been eliminated. The removal of underbrush in Horseshoe Lake Game Preservation near Cairo, Illinois, which contained the only examples of cypress and later successional stages in public ownership (except at Reelfoot Lake) was also mentioned.

The several resolutions (*ECOLOGY* 17: 317-319, Res. 7) prepared during 1935 and calling for buffering of National Parks and the setting up of buffered Nature Sanctuaries in the National Forest and Public Domain were forwarded to the heads of several governmental agencies named and appreciative replies received as follows:

Harold L. Ickes, Secretary of Interior, stated that they were receiving recommendations for enlargement of parks and recognized the advisability of cooperating with other federal and state agencies. Acquisition of lands and other parks was hindered by practical difficulties but all possible support would be given to the movement the committee proposes.

Arno B. Cammerer, Director of National Park Service, agreed with the suggested enlargements and mentioned that the southwestern New Mexico area had been under consideration. He indicated that everything possible will be done for the Great Smoky National Park.

The Acting Chief of the Forest Service called attention to the fact that some form of compensation would have to be provided for residents of the buffered forest.* The Chief of the Forest Service expressed regret at the violations by the CCC camps and stated that they are particularly sensitive to the opinion of members of the Ecological Society.

The Chief of the Biological Survey believed that many of the suggestions are possible of realization and stated that the Biological Survey is deeply interested in protecting wild life and is also interested in our suggestion on Wichita Mountain Wild Life Refuge. He stated they were already co-operating with other Government agencies.

Considerable correspondence was carried out to secure chairmen of committees to urge the buffering or improvement of the several parks. The following were secured: Yellowstone Park, J. W. Scott; Great Smoky National Park, R. E. Coker originally appointed, resigned, E. B. Powers succeeded; enlargement of Wichita Wild Life area, A. O. Weese; the Idaho Primitive area, Arthur Svihla, chairman, taking one year leave, T. C. Frye, acting chairman for 1936-37; the Uinta area, Vasco M. Tanner; Wind River area, S. B. Locke; protection of carnivores in Isle Royal National Park, Sigurd Olson; Southern Arizona and New Mexico Desert Plains Grassland area, C. T. Vorhies invited to act; Big Bend area (Texas), G. W. Goldsmith; and Lassen and Yosemite Parks, T. I. Storer has been invited to act.

There has been concern lest the prairie dog be extirpated over so much of its range as to be unavailable in several states. The local grassland committee for North Dakota has found a good colony near Killdeer, North Dakota, reported by Dr. Stevens, which should be included in a State Park. A committee was appointed for South Dakota with Dr. W. H. Over, chairman. Professor Churchill (state representative) reports that a prairie dog town has been set aside in the Bad Land Forest Preserve.

A number of mimeographed copies of the resolutions accompanied the copies especially addressed to the officials. These were forwarded before President Roosevelt's Wild Life Conference assembled in Washington. V. E. Shelford (chairman) and Dr. R. E. Yeatter (secretary) were appointed delegates to this conference by President Cooper. Dr. Yeatter presented the following resolution to the Conference chairman:

Be it resolved that the North American Wild Life Conference,

1. Approves and urges (a) the establishment of zones of complete protection for roaming animals around the larger National Parks and Monuments and corresponding reserves in Canada and Mexico, covering lands in partial use for tree growing, water shed protection, etc., and (b) the setting aside of similar zoned areas in National Forests, Public Domain and corresponding public lands in Canada and Mexico, to complete the preservation of all types

* This is not necessarily true if residents are willing to leave roaming animals unmolested.

of biotic communities and to include representatives of all the species of wild life.

However, no resolutions were passed by the Conference as a whole. Efforts were made to have the game technicians affiliate with the Ecological Society. The chairman participated in the session on endangered and vanishing animal species and stressed the point that natural biotic communities are *not renewable resources* and should be kept out of such a category in the organization of governmental bureaus. Attention was called to fact that a questionnaire sent to the members of the Ecological Society showed a large experienced group *unanimously opposed* to the inclusion of National Parks and Sanctuaries with agriculture which is *fundamentally concerned with modification* of nature and culture of exotic species. All Canadians consulted, fifteen in number, were strongly of this opinion.

A request from the Department of Interior for an opinion in the matter of the use of very large quantities of poison on the Public Domain in southeastern Arizona and southwestern New Mexico was answered by the chairman who opposed the use of poison and recommended biological control experiments.

Early in March an appropriation item providing for a tunnel through Rocky Mountain National Park to conduct water from Grand Lake to irrigate land in northeastern Colorado was added by Congress as a rider on the Department of the Interior Appropriation Bill. Word came from Dr. Griggs to urge local societies and Ecological Society members to oppose the rider at once. A suitable letter was addressed to 513 local societies signed by Dr. Yeatter and a similar letter merely multigraphed was sent to 400 members of the Ecological Society with typed signature of the chairman. These were sent out within 72 hours of receipt on the suggestion. The bill did not pass, though the number of protests is not known as there was no request to inform the committee of the action taken.

Things do *not always* go smoothly with the campaigns of this kind—there are viewpoints which differ from those of the committee and protests are received and require answers.

There are several schemes to take water from the Yellowstone Park in two or more directions, a proposed tunnel and sequelae probably being most dangerous. The western leaders often sincerely hold ideas detrimental to wild life based on erroneous concepts.

They conceive of the Yellowstone project in the following terms:

"There has been a suggestion made, however, that something be done to protect the Park from the damage done each year by flood waters draining into Yellowstone Lake and which inundate many acres and leave a broad expanse of unsightly shore line. This can be accomplished by constructing a drainage tunnel with its entrance at the level of the natural level of the lake and incidentally, these flood and detrimental waters in the Park can be

put to beneficial uses outside the Park as the good Lord probably intended they should be." This stabilization would make Yellowstone Lake a large City Park Lagoon.

On January 3, a bill was introduced in the House of Representatives to open the Glacier Bay National Monument, Alaska, to mining. The damage to the biological features caused by mining is likely to be heavy. This area was set apart by Presidential proclamation in 1925 in response to a campaign sponsored by the Ecological Society and supported by many national and local organizations. The movement to legalize mining in the Monument is said to have been initiated because of its alleged heavy mineralization and accessibility and a desire to revive the industry in Alaska.

The Ecological Society, having been instrumental in the establishment of this Monument, has a responsibility in defending it from such damage. The chairman accordingly reappointed those members of the original subcommittee of the Committee on Preservation of Natural Conditions who are available, with instructions to take whatever measures seemed necessary in the emergency. The reconstituted committee consists of W. S. Cooper, chairman, C. C. Adams, and R. F. Griggs. Mr. Barrington Moore, who was a member of the original body, now lives in England.

The chairman of the subcommittee made a trip to Washington to interview officials of the Park Service and other interested parties, and immediately thereafter a campaign was undertaken, in which the principal feature was the sending out of several hundred letters to organizations and individuals interested in the maintenance of Federal standards, asking that protests be sent to the Committees on Public Lands of the House and Senate. So far, we know that more than one hundred and fifty complied with our request. The progress of the bill was temporarily stopped but unfortunately, however, it was rushed through at the close of the session on a personal appeal by the Alaska sponsor to the President and members of Congress. This overrides the settled policy of the Federal government regarding National Parks and National Monuments and a campaign to counteract such legislation is needed.

The committee has had several calls from emergency and new government agencies for the nature sanctuary memorandum.

The chairman's term of office expires at the close of the Atlantic City meeting and due to pressure of other duties he finds it necessary to resign as chairman of the committee. Thanks is due the several members of the committee since 1930 for their prompt cooperation in the preparation of official letters.

FINANCIAL REPORT FOR 1936

Receipts

Balance forward		\$ 18.60	
Contributions of organizations			
American Museum	\$10.00		
Cranbrook Institute	2.00		
Connecticut Bot. Society	5.00		
Wild Flower Pres. Soc. Ohio	1.00		
Wilson Ornithological Club	2.00	20.00	
Contributions of individuals			
J. Grinnell	\$ 5.00		
E. S. Hathaway	2.00	7.00	
Royalties, Naturalists' Guide		16.40	
Service provided through chairman		101.00	
Contributions of chairman		22.00	
Ecological Society of America,			
Rocky Mountain Tunnel Campaign		46.68	
V. E. Shelford, travel expenses		15.00	
W. S. Cooper, Glacier Bay Campaign		50.00	
W. S. Cooper, travel expenses		150.00	\$446.68

Disbursements

Typing, mimeographing, printing and supplies	\$163.04		
Postage and telegrams	21.96		
Rocky Mountain Tunnel Campaign	46.68		
Travel, V. E. Shelford	15.00		
Glacier Bay Campaign, W. S. Cooper	50.00		
Travel, W. S. Cooper	150.00	\$446.68	

The entire report is respectfully submitted.

V. E. SHELFORD,
Chairman

REPORT OF THE COMMITTEE ON THE PRESERVATION OF NATURAL
CONDITIONS FOR CANADA AND NEWFOUNDLAND

The Committee on the Preservation of Natural Conditions for Canada and Newfoundland (established in 1932) is composed of the following members: Dr. J. R. Dymond, Royal Ontario Museum of Zoology, Toronto, Ontario, Chairman; Dr. R. J. Bean, Halifax, Nova Scotia; Dr. H. G. Crawford, Ottawa, Ontario; Dr. W. P. Fraser, Saskatoon, Saskatchewan; Dr. C. D. Howe, University of Toronto, Toronto, Ontario; Dr. G. C. Piche, Quebec, Quebec; Professor G. F. Sleggs, St. John's, Newfoundland; Dr. George J. Spencer, Vancouver, British Columbia.

The chairman reports that the Committee has been more active during the past year than previously. Efforts are now under way to bring together information on all the different types of reserves in the country. This com-

pilation is only partially completed but the various governments have shown themselves ready to cooperate and there has been some preliminary discussion of the possibility of setting aside nature sanctuaries in the centre of some of the parks.

In connection with the summer meeting of the A. A. A. S. in Ottawa in 1938, it is suggested that advantage be taken of the occasion to have a discussion with government officials concerned in the administration of National Parks and reserves. Perhaps a symposium on some such subject as the Preservation of Nature could be arranged at which ecologists and government officials could discuss the matter from their respective points of view.

Respectfully submitted,

(signed) J. R. DYMOND, *Chairman*

The report was accepted.

REPORT OF THE COMMITTEE FOR THE STUDY OF PLANT AND ANIMAL COMMUNITIES

(Established in 1931)

The local committee appointed by the President of the Ecological Society in 1935 to further the securing of facilities for grassland study (see report for 1935) has prepared detailed reports on the land needed, and has provided maps giving location and probable cost. This surveying and mapping has occupied the attention of the committee during the first half of the year. A report was filed with the National Research Council in June. The officers of the Council are convinced that the land which the midwestern universities should have near at hand must be obtained by the universities through gifts or purchases. The chairman of each local committee was urged to start a campaign with the alumni to secure gifts with which the land could be purchased and to get provisions inserted in the budget of his university providing for the purchase of the land. A plan has been submitted to the National Research Council for asking granting bodies to provide at least one-third of the needed funds. The success of the several local committees has not been reported.

The buffering of a series of National Parks and the setting up of a series of Buffered Sanctuaries, not provided for in the National Park System in the United States, was suggested last year (see report of the Committee on Preservation of Natural Conditions).

The committee has prepared a map and a list of National Parks and Reserves in North America, including Mexico, and has asked for suggestions as to buffering and otherwise improving them, the idea being to propose a series of sanctuaries suitable for buffering, which may be urged by the Society. It is further proposed that small but excellent pieces of biotic community be preserved where possible by the Federal government under a suitable heading such as Primaeval National Monuments (in the United States) suggested for the Lynn Fork (Kentucky) Deciduous Forest in 1935.

The following series of Primaeval National Monuments was suggested for the United States: (1) East Kentucky Deciduous Forest (Lynn Fork); (2) Magnolia-Bay-Holly; (3) Cypress Swamp, Pearl River Delta; (4) Sage Brush Desert; (5) California Chaparral; (6) Vegetation near Brownsville, Texas; (7) Joshua Tree (in California); and (8) Smith Island live-oak-palmetto, North Carolina (sponsored by B. M. Wells).

Mexican National Parks were located on our map as circles only and were transferred from a map provided by Ing. J. Manuel Corona, Departamento Forestal, Mexico, and no comments were received. Those relative to areas in Canada and Newfoundland are being forwarded to Chairman Dymond of the Canadian Committee.

Respectfully submitted,

V. E. SHELFDOR, *Chairman*

The report was accepted.

REPORT OF THE CONFERENCE COMMITTEE

As a result of discussion by Francis Ramaley and of a special Conference Committee headed by A. H. Wright, the following by-law was presented regarding the work of the Committees of the Society on Conservation and Study of Communities under Natural Conditions:

New By-Law. The Society shall maintain three permanent committees as follows:

- I. *A Committee on the Preservation of Natural Conditions* shall operate in two sections; one for the United States and one for Canada and Newfoundland. Its duties shall be to initiate and carry out action concerned with preservation of natural conditions.

Subcommittees to further certain projects may be appointed at any time by the chairmen of either section with the approval of the President of the Society.

1. The organization of the section for Canada and Newfoundland (established in 1931) shall be determined by the Canadian members with the approval of the Executive Committee of the Society.
2. The section for the United States shall be organized as follows:
The Committee on Preservation of Natural Conditions for the United States (established in 1917) shall consist of an executive group composed of a chairman and two or more other members and of representatives in the several states and other similar units. It shall maintain an up-to-date list of names and addresses of officers of local societies interested in the field of its activities.

- II. *The Committee on Applied Ecology* shall consist of a chairman and two

or more other members. Its duty shall be to cooperate with governmental and other agencies in matters where basic ecological principles may assist in the solving of economic problems.

- III. The *Committee for Study of Plant and Animal Communities* shall consist of a chairman, the chairmen of the two preceding committees, *ex officio*, and other members representing different regions of North America and different scientific interests. Its duties shall be to act as a fact finding body and to advise the Society and the two preceding committees, when called upon to do so as to general policies and particular problems.

The chairmen of the three committees shall be elected by the Society for terms of three years, except that the original appointments shall be made by the President for terms of three years, two years, and one year respectively. Interim appointments shall also be made by the President. The chairmanships of the first two committees may at any time, if deemed advisable, be vested in one person. All other members of the committees shall be appointed by the President on the request of the respective chairmen.

No person in the service of the federal government of the United States shall be eligible for membership in the executive group of either of the first two committees.

The chairman of one of the committees shall be elected to become a member of the Executive Committee of the Society annually for a term of one year.

The committees shall be furnished with such needed financial support as the funds of the Society may warrant.

ACTIONS BY THE SOCIETY

The motion to accept the report of the Committee and to adopt the by-law was carried without a dissenting vote and subsequent actions unanimously elected the following:

- A. O. Weese, Chairman of the Committee on Preservation of Natural Conditions.
- H. C. Hanson, Chairman of the Committee on Applied Ecology.
- V. E. Shelford, Chairman of the Committee for the Study of Plant and Animal Communities.

Under the by-law the terms must be arranged by the President to run one, two, three years to provide alternate expiration.

Later action elected A. O. Weese a member of the Executive Committee for one year.

The Secretary-Treasurer then asked the Society to take the necessary steps to separate the secretaryship from the treasurership as the consequence of the growing demands upon his time. It was moved by V. E. Shelford that the incoming officers are instructed to draft and publish an amendment

to the Constitution of the Society separating the office of Secretary and of Treasurer and fixing the term of office so that both will not expire in the same year. A three year term was recommended. The motion was seconded by G. D. Fuller and passed without dissenting vote.

It was moved by V. E. Shelford that the incoming officers are instructed to draft a modification of the Constitution authorizing Organization memberships. The annual dues of the Organization Members should be from two dollars to ten dollars or more, as elected by the organization. They will receive the Bulletin of the Society, and the reprinted report of the Committees described under the by-law. By "Organization" is meant all kinds of organizations interested in the preservation of nature and application of ecological principles, such as universities, colleges, museums, and institutions of similar nature. The motion was seconded and passed without dissenting vote.

It was moved by V. E. Shelford that the Treasurer, or Secretary-Treasurer, be instructed to provide a proper space of printed matter on all cards calling for the dues, inviting members to make voluntary contributions to the support of the Committees described under the new by-law, setting up the three Committees authorized at this business meeting. The motion was seconded and adopted without dissenting vote.

V. E. Shelford called the attention of the Society to a failure to comply with a contract with Williams and Wilkins Publishing Company. The Secretary was requested to secure the publication of the required notices concerning "The Naturalists' Guide to the Americas."

It was moved by V. E. Shelford that one hundred dollars be allotted for the Committee on Preservation of Natural Conditions, and one hundred dollars be allotted for the Committee on Applied Ecology, and that royalties of the Naturalists' Guide and all contributions from members and organizations be assigned to the three Committees.

The motion was lost. A substitute motion by R. F. Griggs was made to refer the allotment of funds to the above named Committees to the Executive Committee. The substitute motion passed unanimously. The portion of the lost motion, however, referring to the royalties of the Naturalists' Guide and contributions from members and organizations was adopted informally.

ORGANIZATION OF A WESTERN SECTION

The following by-law was prepared by W. S. Cooper and in his absence read by Orlando Park:

"The Western Division of the Society shall include those members residing west of the eastern boundary of the State of Colorado. Its purpose shall be to further the aims and interests of the Society in the western States. Management shall be vested in an Executive Committee of three members, the chairman of which shall be the executive secretary of the section. The chair-

man and members of the Executive Committee shall be elected by the Division, and shall serve for a period of two years. The Secretary-Treasurer of the Society shall furnish to the Executive Secretary of the Division from time to time the names and addresses of members of the Society residing within the territory of the Division. Necessary clerical and incidental expenses of the Western Division shall be paid from the treasury of the Society, and programs and abstracts shall be published in the Bulletin of the Society."

The adoption of the above by-law was moved by G. D. Fuller and seconded. In discussion following by C. F. Korstian, C. C. Adams, and V. E. Shelford, some objection was made to the delimitation of the eastern boundary of the western division, and it was moved and seconded that the Executive Committee be given the power to adjust this matter. The by-law was unanimously adopted.

(The Executive Committee acting on these instructions subsequently modified the by-law to read: "The western division of the Society shall include those members residing west of the eastern boundary of the State of Colorado, and others who wish to be so recorded." The remaining portion of the by-law was left as stated above.)

REPORT OF THE COMMITTEE ON AFFILIATION WITH THE AMERICAN SOCIETY OF WILD LIFE SPECIALISTS

The Committee on Affiliation consisting of W. S. Cooper, Chairman, Chancey Juday, and Orlando Park, met with a committee representing the American Society of Wild Life Specialists at Madison, Wisconsin, on November 19, 1936. Following this meeting a plan for affiliation was drawn up by W. S. Cooper, and in the absence of the Chairman of the Committee this report was presented to the Society by Chancey Juday as follows:

Plan for the affiliation or amalgamation of the Society of Wild Life Specialists with the Ecological Society of America as a section thereof:

Organization. Sectional affairs are to be in charge of a Committee of Three, consisting of a Chairman, a Vice-Chairman, and a Secretary of the Wild Life Section. The Section Chairman is to be a Member of the Executive Committee of the Ecological Society.

Expenses. Postage, clerical and other incidental sectional expenses are to be paid from the treasury of the Ecological Society.

Meetings. The Wild Life Section is to hold a meeting annually with the Ecological Society at the time of the latter's annual meeting and at such other times and places as the Section may desire.

Journal. A new journal is to be established which is to be devoted to the economic aspects of ecology; the exact title of the journal and other relevant matters are to be decided by a joint committee from the Ecological Society and from the Wild Life Section. The journal is to have its own editorial board which is to be elected by the Ecological Society with the

recommendation of the Wild Life Section. All three journals of the Ecological Society, namely *ECOLOGY*, *ECOLOGICAL MONOGRAPHS* and the proposed new journal are to be open to all members.

Dues. The annual dues of the Wild Life Section are to be one dollar for general Ecological Society maintenance, plus subscriptions to *Ecology* or to the proposed journal. Subscription to the new journal is to be \$3.00 to members, thus making the minimum of dues and subscription to the members of the Wild Life Section the same as those of active members of the Ecological Society. In addition to the required subscription to *ECOLOGY*, or to the proposed new journal, members of the Society may subscribe to our other periodicals at the following rates:

ECOLOGY, \$3.00; *ECOLOGICAL MONOGRAPHS*, \$6.00; the *NEW JOURNAL*, \$3.00. The Wild Life Section is to be financially responsible for the founding and maintenance of the proposed new journal.

It was moved by W. C. Allee that the report of the Committee on Affiliation with the Wild Life Specialists be accepted in principle and the details be referred to an appropriate Committee to be appointed by the incoming President. The motion was seconded and carried without a dissenting vote.

R. E. Griggs recalled to the attention of the Society the critical condition of *Biological Abstracts*, and a prolonged discussion ensued. It was moved by H. I. Baldwin that a voluntary assessment of one dollar, under similar terms as voted by the Botanical Society of America, be levied on the membership of the Ecological Society of America for the support of editorial work of *Biological Abstracts*. The motion was withdrawn and the matter was referred to the Executive Committee by J. G. Needham with the power to act.

H. I. Baldwin then moved that all members of the Ecological Society of America be urged to advise the institutions with which they are concerned to maintain subscriptions for *Biological Abstracts*, and that members of the Ecological Society of America subscribe individually to *Biological Abstracts* if possible.

REPORT OF THE COMMITTEE ON NOMENCLATURE

Several reports have been mimeographed by your Committee on Nomenclature. It is now time for the Society to decide whether it wants the material printed or mimeographed as a preliminary list. This should not be done until the material has been thoroughly edited, and the forest soil terms included by a representative Committee of members who have sufficient time and interest to devote to this.

Respectfully submitted,

HERBERT C. HANSON, *Chairman*

The report was approved and the Committee was continued.

It was moved by C. C. Adams that the incoming officers of the Ecological Society of America communicate with the officials of the Society of American

Geographers for a joint meeting next year. W. C. Allee moved to amend this motion to read that the incoming officers of the Ecological Society communicate with the officials of the Society of American Geographers for a joint meeting next year or at some early future date. The amendment was seconded and carried.

It was moved by C. C. Adams that the incoming officers appoint a Committee to investigate the possibilities of a library which should become the repository for historic materials concerning the Ecological Society of America, the materials to remain the property of the Society at least for the present. The motion was seconded by A. H. Wright and carried.

It was moved by H. C. Hanson that the Society express its appreciation of the services of the Secretary-Treasurer, Dr. Orlando Park; and that the Secretary write President William S. Cooper expressing the appreciation of the Society for his careful and constructive leadership during the past year. The motion was seconded and carried.

A resumé of a resolution discussed by the Society and referred to the Executive Committee. This resolution was subsequently received by the Secretary from V. E. Shelford as follows:

WHEREAS: The attention of the Committee on Preservation of Natural Conditions has been called to the wanton destruction of wild animals of all sorts through the operation of agencies in so called "Vermin Campaigns."

Be it resolved: That the Ecological Society of America go in record as condemning such campaigns and that its members be urged to give wide local publicity to the serious results of such campaigns.

Be it resolved: Further that Dr. A. M. Reese of the University of West Virginia be requested to prepare and publish articles calling attention to these matters which may be used by interested persons to further this program throughout the country.

REPORT OF THE COMMITTEE ON NOMINATIONS

Your committee submits the following candidates:

For President: R. E. Coker, North Carolina.

For Vice-President: H. de Forest, Southern California.

For Secretary-Treasurer: Orlando Park, Northwestern.

For the Editorial Board of Ecology: Walter Mosauer, Thomas Park, A. G. Vestal, and J. M. Aikman.

For the Editorial Board of Ecological Monographs: G. P. Burns and C. H. Kennedy.

Respectfully submitted,

W. P. TAYLOR, *Chairman*

W. C. ALLEE

G. D. FULLER

There being no nominations from the floor it was moved, seconded and carried that the Secretary be instructed to cast the vote of the Society for the list of officers presented by the Committee on Nominations and that the recommendations of the committee be approved.

The vote was cast and the persons named were declared elected as officers of the Society for the coming year.

The meeting was adjourned at 12:15 P.M.

ORLANDO PARK, *Secretary-Treasurer*

NOTES AND COMMENT

ON SELF-RECOGNITION AND SOCIAL REACTION IN RELATION TO BIOMECHANICS, WITH A NOTE ON TERMINOLOGY

In some previous attempts to analyze certain aspects of so-called social behavior in fishes, the question of the possibility of self-recognition in such forms kept cropping up in the writer's mind, but was left untouched in the hope of future opportunity to delve more deeply into this particular problem. However, the postponement of such opportunities seems indefinite and it may therefore be desirable to present a first approach to a solution which can be made in a purely deductive manner from a simple consideration of biomechanics, from which the experimental work must lead on.

It is evident that self-recognition is a collective term covering two interrelated but nevertheless quite distinct concepts which we might designate as the concept of individual self-recognition and of social self-recognition. Since the two categories are in part antithetic they had better be considered separately.

RECOGNITION OF SELF AS A BODY APART AND DISTINCT FROM OTHER BODIES (INDIVIDUAL SELF-RECOGNITION)

In mechanism of individual self-recognition is that of the supernumerary ($n + x$) sensations of an event involving the body of the perceiving organism as compared with a lower number of sensations (n) received from the identical type of event happening to a body apart.

Thus, when we touch our legs with our hands, we receive a double sensation of touch, one from our fingers and one from our legs, whereas by touching a foreign object we receive only one set of sensations, namely from our hands. If we also observe the event with our eyes, we get three perceptions of a contact between our hands and our legs, but only two perceptions of a contact between our hands and a body apart. Such instances can, of course, be increased indefinitely.

In this manner individual self-recognition develops as a simple system of associations between perceptions in different sensory categories or of multiple sensations in the same category. Self-recognition thus developed must therefore also be limited to self-recognition in those sensory categories in which either multiple self-perception within the category or in association with other sensory categories is possible. If a sensory category is excluded from the possibility of such multiple or associated self-perceptions, it is therefore also excluded as a sensory category of self-recognition, even if it exists as a category of perception of other bodies.

Here we immediately arrive at a critical point in the problem of self-recognition in fishes and similar organisms. The possibility of self-recognition in the visual category rests upon the ability of bringing the body of the perceiving organism within its own field of vision, *e.g.* by craning the neck, etc. If we now consider the comparatively rigid body of a mackerel with its lateral flushly-embedded eyes, we immediately realize the physical impossibility of visual self-perception. The individual self-recognition of the mackerel must, in spite of its excellent vision of other objects, be virtually that of a blind organism.

So far we have dealt with individual self-recognition as the system of discreet associations between multiple perceptions in various sensory categories. The question then arises as to the degree of integration of these various forms of self-recognition in discreet association groups into a recognition of the entire physical self as a whole. It is obvious that the various types of sensations have very different potentialities as mechanisms for

the integration of individual self-recognition. Thus, for instance, hearing or taste and smell could only provide integration of self-recognition (in association with localized sensations of touch, etc.) for very limited parts of the entire self. Musculature and temperature sensations offer somewhat greater possibilities in that they involve much greater portions of the body; but they would probably not be able to provide very sharp definitions.

The sense of touch has still greater potentialities, but it is important to remember that these potentialities are to a large extent dependent upon the mechanical ability to achieve the sensation of the double touch. That is, they require the presence of antennae or flexible limbs capable of exploring the body by the sensation of touch. If we now consider the mackerel again, we realize that the possibility of integrating its individual self-recognition by this sensation is limited to the extremely small portions of its body in which it can achieve the perceptions of double touch between the paired ventral and pectoral fins and its flanks. The mackerel's ability of achieving integrated recognition of itself as a whole is thus for purely mechanical reasons confined to the potentialities of a virtually blind organism practically without the sensation of touch.

Finally, there can be no doubt that the greatest potentialities for integrated self-recognition are presented by the visual sensory system when the mechanical possibility for self-perception is adequately provided (in humans it is further aided and complicated by external means such as mirrors, etc.). On this point we have already seen that the mackerel is quite deficient.

To illustrate the actualities of these speculations we might mention that a blind organism would not be able to integrate a permanently numb limb in its self-recognition of the whole. The converse situation is illustrated by pains felt in an extracted tooth or amputated limb. Even in humans the recognition of the self as a whole is only fractional and mainly external, by visual and touch integration; while we are actually not cognizant of a great number of our internal parts. If in other organisms, such as the mackerel, neither vision nor touch is mechanically implemented to a perception of the whole, even the external self-recognition must be incomplete and fractional. A young dog chasing its own tail is evidence of even an external self-recognition not yet completely integrated to include the tail. In the dog this integration is subsequently completed, but in many other organisms even the possibility of such completion may not be present.

RECOGNITION OF SELF AS A BODY SIMILAR AND AKIN TO OTHER BODIES (SOCIAL SELF-RECOGNITION)

When we consider the gregarious or social behavior of an organism as reactions to the perception of other organisms of its own kind, it becomes an obligation first to investigate whether the organism in question is potentially capable of reacting in those terms, that is to say, their capacity to conceive of themselves as similar and akin to the other organisms to which they thus react. It is obvious that the requirements for such a performance is the ability of the organisms to see itself as others see it in terms of any or all of its sensory categories. That is to say, it is dependent upon the quality of its individual self-recognition in the sensory category in which it reacts to the perception of other organisms of its kind. In the case of a mackerel, the writer has found that exclusion of visual perception also excludes its gregarious schooling reactions. But we have already discussed the inability of the mackerel to obtain an integrated visual recognition of itself. In consequence, the reaction of the mackerel to the perception of others of its kind cannot be in terms of a response to individuals recognized to be similar to itself, but must be based upon an automatic association mechanism of a different order in which the perception of another fish similar to itself (it need not even be the same species¹) fits as a key fits into a lock.

¹ Parr, A. E. 1927. A contribution to the theoretical analysis of the schooling behavior of fishes. *Oc. Pap. Bingham Oceanogr. Coll. No. 1.*

It is hardly necessary to enlarge any further upon these speculations which are merely presented because they seem to suggest various promising lines of approach to an experimental study of the development of individual self-recognition and of social reactions by a comparison between organisms of different mechanical potentialities for achieving a partial or integrated sensory recognition of themselves. Thus an eel might for instance be capable of integrated self-recognition both by touch and vision where a mackerel is not and so on and so forth.

NOTE ON TERMINOLOGY

In the earlier paper¹ the writer attempted to interpret schooling behavior in fishes as the mechanical integration of simple automatic responses. In the subsequent article² "schooling instinct" was used as a convenient general term for the automatic reaction complex thus analyzed in the previous publication to which reference was given. Similar use was also made of the terms "sexual instinct" and "feeding instinct," with the intended implication that these were also capable of the same type of analysis as that to which the schooling instinct had already been subjected. This loose usage of language has, unfortunately, led to the misunderstanding³ that the slight advance made in the earlier paper¹ had been "largely abandoned" in the later article. Nothing could ever have been farther from the writer's own intention. When analyzing a single "instinct" or complex of reactions, as in the first article, one may be able to break it down into a system of very simple automatic responses. When analyzing the relationship between different instincts or complexes, one must of necessity use a general term, defined by their separate analysis, since it is not feasible to make a restatement of all its component parts every time a reaction complex as a whole is referred to. Since the much misused term "instinct" has proved confusing in such application, the writer would therefore suggest an entirely new designation: synaprokrisis (*ἀπρόκρισις* = answer) for a definite reaction complex or behavior-pattern unit already interpreted as a purely mechanical integration of simple automatic responses or explicitly believed to be capable of such interpretation. For "schooling instinct," "sexual instinct" and "feeding instinct" in the 1931 paper, one should therefore read: schooling synaprokrisis, sexual synaprokrisis and feeding synaprokrisis.

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THE EEL-GRASS SITUATION ALONG THE MIDDLE ATLANTIC COAST *

Each spring since the extensive, epidemic wasting of the common marine eel-grass, *Zostera marina* L., five years ago, there have been anxiously optimistic reports of its reappearance at numerous points. Correlating these indicates a steady increase in the number of new beds and the extension of refoliated range, but no estimate may be had from them concerning the ecological value of this progress. It is certain that the plant persists abundantly through the summer in only a few localities; usually the leaves, badly spotted and marked by lesions associated with the parasitic *Labyrinthula*, slough away in early summer to leave sparsely developed stems and a few seed producing plants of little significance as winter food for migratory waterfowl, in protecting dependent small

² Parr, A. E. 1931. Sex dimorphism and schooling behavior among fishes. *Amer. Natur.* 65.

³ Allee, W. C. 1934. Recent studies in mass physiology. *Biol. Rev. Cambr. Philos. Soc.* 9 (1): 3. —. 1935. Relatively simple animal aggregations. In: A Handbook of Social Psychology, p. 922. *Clark Univ. Press.*

* Contribution 111, Woods Hole Oceanographic Institution.

animal forms, or in holding the bottom against erosion.¹ Some notable exceptions, the estuaries of Chesapeake Bay, Shinnecock Bay, L. I., and Great Bay, N. H., have been remarked, where thick grass has abounded through the epidemic.² Strangely, the grass in these regions has been heavily parasitized, but seems to grow with such vigor that the wasting has been offset.

The impression gained from investigations of the *Labyrinthula*, the protozoan parasite producing the wasting, is that the presence of plants in the spring is no indication of the bed's continuance through the summer. During the warm months the organism is extremely active and may destroy plants within a few days after spotting or streaking symptoms develop. In anticipating the eel-grass' fate, it would be desirable to know the extent of new beds, the proportion of seedling plants, whether or not the specific parasite is present and active, and seasonal conditions that may be related to vegetative growth.

Early in June, hoping to discover something of these factors, a short intensive, field search was made of the shallow bays from Greenwich, R. I., to Great Bay, N. J. This was made possible through the kind cooperation of Mr. John L. Lynch of the U. S. Biological Survey.

Along the Rhode Island coast conditions for growth seemed much more favorable than farther south. In Narragansett Bay, proper, at Greenwich and Wickford, however, reports and hurried inspection yielded no eel-grass, a matter of concern since the beds had heretofore furnished excellent natural protection to young lobsters introduced from the state hatcheries. At Point Judith, in Fish Pond and westward in Charlestown Pond, Quanochohtaug Pond and Winnapaug Pond, there were scattered plants and small, separated beds from a foot to a yard in diameter. These were in good condition, leaves from ten to fifteen inches long, with only a small proportion showing any symptoms of the disease. Many of these plants, surprisingly, were in seed—an unorthodox condition that applied all along the coast, since it is generally held that *Zostera marina* fruits in mid to late summer following inhibition of vegetative growth by the warming water. Abundant growth of vigorous plants in relatively dense, though scattered beds prevailed in the extensive shallows of the western half of Little Narragansett Bay. The leaves were large—a meter long and a quarter of an inch wide; many plants were in seed. This area presented the most favorable redevelopment observed, though streaking and blackening of the leaves was common.

Along the eastern Connecticut coast the drift and reports indicated scattered beds. In Quimbog Cove and at other points east of Mystic, broad leaves a yard long and numbers of plants in seed, free of symptoms, were found in the drift. But in the deeper, rocky bays near New London, no grass or signs of grass could be found. A number of negative observations were made between Stamford and New Haven.

The situation in the shallow bays on the south coast of Long Island was very puzzling; in these the grass had formerly flourished in great profusion, and since the bottoms are still relatively undisturbed, conditions here would seem exceptionally favorable for seedling plants. Along the western and southern shores of Mecox Bay there were many plants in diffuse beds bearing leaves from eight to eighteen inches long and not so broad as those in Watch Hill Bay, most streaked with brown or black, and many in seed. In a small deep arm at the southeast of the bay a number of very large plants were seen with leaves up to four feet long and three-eighths of an inch broad; these bore the marks of disease.

Dense beds of eel-grass extended from the sandy shoals a hundred yards from shore to the edge of the channel, about half a mile off, along the south of Shinnecock Bay. The leaves were small, from eight to ten inches long and a quarter of an inch wide.

¹ Renn, C. 1936. The wasting disease of *Zostera marina*, I. A pathological investigation of the diseased plant. *Biol. Bull.* 70: 148-158.

² Cottam, C. 1935. The present situation regarding eel-grass (*Zostera marina*). U. S. Dept. Agri., Bur. Biol. Surv. Wildlife Res. Manag. Leaflet BS. 3.

These were much eroded and marked by the disease, yet they formed relatively large beds, five feet in diameter, underlaid by firm mats of stems in good condition. From a tenth to a quarter of the plants in these beds were in seed. The growth prevailed in the southern shallows west to the head of the bay, and was characteristic of the gravelly bottom in western Tianna Bay, joining Shinnecock on the north.

These beds, despite the prevailing symptoms of disease, had apparently persisted through the epidemic. Specimens have been received each year from this area, and the current plants may be traced back to stem stock two seasons old. Similarly, the more scattered plants in Mecox Bay were derived from old stem stock; very few of any plants were seedlings.

The southern shallows of Moriches Bay, and of Quantuck and Ogden Ponds, which connect Moriches with Shinnecock Bay through the Interstate Canal, were entirely free from growing grass. On the wide flats to the north and west of Fire Islands in Great South Bay there were uniformly scattered plants and some very small clumps, but no beds to speak of. These plants, too, were from old stock. They were small and almost altogether free from symptoms of disease—possibly related to their retarded growth through a layer of fresh silt two to three inches deep that covers this area. A few of these plants were in seed. The shallow to the north of the channel from Fire Islands to Jones Beach appeared free of eel-grass, though occasional floating leaves were noted.

In Barnegat Bay, intensively explored along the south shore, there were scarcely any plants, and no small areas comparable to any of the foliated regions of Long Island. Small, spotted leaves and seed plants were found in the drift near Tom's River, but no living plants could be discovered to the north of Barnegat Inlet. About half a mile south of the Inlet, below Barnegat City, there were a few scattered plants, not more than a hundred in all. And on the shallows near Lovelady several small beds were discovered, all plants free from any trace of disease, and bearing narrow leaves about eight inches long. Several seed plants were found among them. Fishermen and clam diggers along the south shore reported the almost complete absence of the grass; shallow trawls came up with few leaves. On the other hand, there appeared to be, even early in the season, a considerable drift of leaves through Barnegat Inlet on the ebb tide, to judge by fouled anchor ropes and fishing lines. But it is certain that very few growing plants have been seen anywhere in the Bay. This is also true of the western shore where a number of searches and enquiries were made, the only successful haul being seven leaves that turned up in an order of steamed-clams, reputedly from Tuckerton Harbor.

Specimens of diseased plants were taken from all beds and examined microscopically for the parasitic *Labyrinthula*, and also for the *Ophiobolus* reported by Mounce, Tutin, and Petersen as present in Canadian, British, and Danish grass.³ The *Labyrinthula* was present without exception in grass showing spotting or streaking. Two specimens from Shinnecock Bay bore a very sparse development of fungus mycelium, but none showed pycnidia characteristic of fungus infection described by the above investigators. The parasite, then, is present everywhere in the area studied, and presumably will become more active through the summer.

A second feature of significance is the scarcity of seedlings in the foliated areas, indicating the ineffectiveness of spreading by seed as compared with growth from persistent stem stock. From this it may be anticipated that long cool springs, favoring the vegetative phase of the plant's development and permitting the storage of food materials in the stem, will greatly accelerate the spread of the beds. Rapid warming of the water, on the other hand, will be unfavorable in shortening vegetative development and stimulating the parasitic activity of the *Labyrinthula*.

CHARLES E. RENN

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³ Mounce, I., and W. Diehl. 1934. A new *Ophiobolus* on eel-grass. *Can. Jour. of Res.* 11: 242.

WINTER ACTIVITY OF THE SKUNK

It is well known that the skunk is a hibernator. Skunks (*Mephitis nigra*) are abroad during the mild spells of winter, and, after the rut, sub-zero weather does not keep the more adventurous individuals denned.

The following notes were made in the Ithaca, New York, region. The data were secured through personal examinations of trapper's catches and unskinned animals bought by local buyers. The sex of more than a thousand specimens was determined; only those on which the exact, or nearly so, date of capture was recorded are used in the tables.

Early November night temperatures of 15–25° F. induce the animals to remain denned for short duration. Usually by mid-December most of the females have hibernated, but it is not uncommon for the males to remain more or less active throughout the winter. Late January brings activity on the part of the females, and sub-zero weather during February will often find skunks abroad. The sexual disparity shown by hibernators and non-hibernators is well indicated in table I, based on captures on which the

TABLE I. *Relative activity of male and female skunks during winter*

Date Winter of 1931–32	Average temperatures (° F.) ¹	Males	Females
Nov. 10–19	54.5	34	41
Nov. 20–29	50.4	29	26
Nov. 30–Dec. 9	32.3	21	5
Dec. 10–19	39.7	16	5
Dec. 20–29	35.2	18	2
Dec. 30–Jan. 8	34.1	8	0
Jan. 9–18	41.4	14	2
Jan. 19–28	36.6	1	19
Jan. 29–Feb. 7	30.4	3	15
Winter of 1933–34			
Nov. 10–19	26.5	8	1
Nov. 20–29	35.2	20	3
Nov. 30–Dec. 9	37.5	31	7
Dec. 10–19	27.1	23	0
Dec. 20–29	24.0	6	0
Dec. 30–Jan. 8	29.0	19	0
Jan. 9–18	31.3	13	3
Jan. 19–28	29.6	2	11
Jan. 29–Feb. 7	12.6	0	6

¹ Temperatures taken at the U. S. Weather Bureau Station, Ithaca, New York. The field investigations were carried on in areas which have average temperatures 1 to 3 degrees lower.

sex was determined during the 1931–32 and 1933–34 seasons. It indicates rather clearly the tendency of females to hibernate early in winter. The date of entrance into hibernation is manifestly governed by the temperature. This is well indicated during the mild winter of 1931–32 and the severity of early winter in 1933. Low temperatures then, would seem to be the exciting cause of winter sleep.

The small number of males taken during late January and February may be explained, in part, by the large numbers trapped earlier in the winter. There is likewise a segregation of sexes, for some dens have yielded as high as 8 females and no males. Other dens have produced 6 and 5 females respectively, while no males were taken from these same dens.

Adult individuals have been known to remain in the den for six weeks at a time.

One skunk which the writer had under observation hibernated in a culvert on December 24, 1935, and did not venture out until February 5, 1936, a total of 44 days. This is exceptional, for even the females rarely spend more than a month at any time in sleep.

The active males feed during late December and January on dried fruit drupes, insects, small mammals, grains, grasses, carrion and garbage. In spite of low temperatures, enough is eaten to minimize the weight loss which is characteristic of hibernating animals. This is indicated in table II, which discloses the greater loss of the hibernating females.

TABLE II. *Loss in weight of skunks during winter*

	Weight Nov. 10-15	Weight Jan. 25-Feb. 10	Per cent loss in wght.
Males	5 lbs. 14 oz. (107) ²	5 lbs. 1 oz. (43)	13.8
Females	5 lbs. 12 oz. (121)	3 lbs. 9 oz. (30)	38.0

² Figure in parenthesis indicates number of animals weighed.

For the entire winter of 1934-35 careful observations were made on a series of six occupied skunk dens. Straws were so placed that any exit or entrance of an animal to the den could readily be determined. From December 8 to 12, during an unseasonal cold spell (nightly temperatures of 6, 3, 5, 4 and 15° F.) the animals did not move. On the other hand, night temperatures of -16° F. during the last week of February, 1936, did not daunt the animals, for their characteristic tracks were everywhere. This may be explained by the mating urge.

Mating occurs during late February and early March in central New York, although some years it may occur as early as mid-February. The males apparently are polygamous and travel widely during this season. The writer has heard skunks, both in dens and under buildings, squealing and fighting during the first week in March. The second week of March, 1936, the animals were still calling and fighting, which Wight³ states is an apparent indication of sexual activity.

Young of the year are seldom trapped during the winter. Irrespective of sex, they enter hibernating quarters with the first cold snap, and frequently remain denned until mid-March. Perhaps one in a hundred appear in the fur-buyer's hands. Pelts of these young animals are characteristic. Not only are they small, but always unprime, and frequently with much less fat than the large pelts exhibit. It is probable, because of the prolonged hibernation, that many of the yearlings do not breed.

SUMMARY

A study of hibernation of the skunk in central New York was conducted during the winters of 1931-32 and 1933-34. Females are confirmed hibernators; males are more or less active throughout the winter. Low temperatures appear to be the exciting cause of winter sleep. During the mating season, sub-zero temperatures fail to keep skunks in their dens. The data suggest a segregation of sexes during hibernation. While individual adults rarely hibernate for more than a month at a time, immature animals usually sleep throughout the winter, rarely venturing from their dens until mid-March. During winter, males show an average loss of one-seventh of their weight, females a loss of approximately two-fifths their weight.

W. J. HAMILTON, JR.

CORNELL UNIVERSITY

³ Wight, H. M. 1931. Reproduction in the eastern skunk. *Journ. Mammalogy* 12 (1): 42-47.

BURIED FORESTS IN BOGS OF SOUTHWESTERN IRELAND—A CORRECTION

In a note under the above title on page 169 of the January issue of this journal, 6th line from the bottom instead of "the change from Sub-boreal to Atlantic climate around 10,000 B. C." read "the change from Sub-boreal to Atlantic climate around 1,000 B. C." Some authorities place the date of this change around 700 B. C.

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EFFECTS OF DROUGHT ON VEGETATION NEAR MILES CITY, MONTANA

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The widespread drought of 1934 was the most severe in the recorded history of southeastern Montana. Its effects on the people, who depend chiefly upon livestock raising, may be inferred from the fact that between June 1, 1934, and June 10, 1935, in addition to the cattle and sheep disposed of through ordinary channels, three hundred and fifty thousand drought-relief cattle were purchased by the Government in thirty-eight Montana counties at a total cost of over five million dollars. More than half the cattle in Custer County, in which Miles City is situated, were so purchased.

The observations presented in this paper were made in the vicinity of Miles City, mostly on moderately grazed land of the U. S. Range Livestock Experiment Station of the Bureau of Animal Industry, where cooperatively the Forest Service is conducting range studies.

WEATHER CONDITIONS

About three-fourths of the annual precipitation at Miles City falls during the growing season, April through September. Summer rainfall in 1934 was only 3.53 inches, as compared with the 57-year average of 9.32 inches. Of the 57 crop-years, that is, years reckoned from the end of the previous to the end of the current growing season, precipitation in only one, 1931, was less than in 1934. Table I shows the distribution of the 57 years by one-inch rainfall classes.

TABLE I. *Frequency table of precipitation at Miles City, 1878-1934 inclusive, from U. S. Weather Bureau records. Summer (April-September, inclusive) and annual (October 1 of prior year to October 1 of current year)*

Inches	4	5	6	7	8	9	10	11	12	13
Summer	3	1	6	3	9	14	4	4	6	3
Annual			2			2	6	9	7	8
Inches	14	15	16	17	18	19	20	21	22	Average
Summer	2			1	1					9.32 in.
Annual	5	5	5	2	2	1		2	1	13.24 in.

The seasons in the two lowest summer classes are 1897 (4.30 in.), 1924 (4.57 in.), 1931 (4.00 in.) and 1934 (3.53 in.), and in the lowest annual class, 1931 (6.21 in.) and 1934 (6.34 in.). Thus it is seen that the two driest years and three of the four driest summers have occurred in the eleven-year interval, 1924–1934. Parenthetically, the drought year 1936, the effects of which have not become fully apparent at this writing, had only slightly more rainfall (summer 3.58, annual 6.66 in.) than 1934. The only soil moisture measurements available from 1934 are 10 samples taken from a sandy loam soil on August 14, after showers on the 10th and 11th. At the 3-inch level, soil moisture ranged from 3.79 to 4.98 per cent, and at the 9-inch level from 4.67 to 6.08 per cent of dry weight.

The drought was aggravated by the highest monthly temperatures ever experienced. Beginning in June 1933, and extending through an open winter and an early spring, temperatures were above normal every month, except December, up through August 1934.

EFFECTS ON WOODY PLANTS

In the summer of 1935, yellowing foliage and dead individuals in many stands of pine and juniper attested the severity of the drought on upland trees, and 1934 diameter increments were, in the main, less than those of other years. In many stream bottoms tracts of cottonwoods had been injured and even killed, as in figure 1. Nearly all trees in the picture exhibit some injury, but the heaviest is mostly on higher ground where the original stand of trees and undershrubs was only half as dense as near the river. Previous dry years, especially 1931, have probably contributed to the damage.

Artemisia cana, although to be found growing on the uplands, is most abundant in coulees and bottoms. Figure 2, a view down such a bottom, shows the injury to a practically pure stand of this species. Not all the bushes in the foreground and middle distance are completely killed. Unlike *A. tridentata* in this locality, *A. cana* sprouts readily after the tops have been killed to the ground. Figure 3 shows a bush making rapid regrowth in this manner.

On three sample strips across the bottom between the fence and the foreground in figure 2, about three-fifths of the bushes had been killed back to the ground and only one per cent of the original volume of these had regenerated by October 1935. Of the remaining two-fifths, which had been less severely injured in 1934, about 30 per cent of the leafage was in evidence. Most of the injured bushes in figure 2, then, were not making such vigorous recovery as the bush pictured in figure 3.

To study the behavior of *A. cana* in an upland site in association with *A. tridentata*, a transect was laid out on a gentle north-facing slope. It extended from clay at the lower end, progressively into sandier soils, from a low growth of *A. tridentata* across an intermediate area largely given to *A. cana*, and

ended in a stand principally of *A. tridentata*. The upper and lower thirds of this transect included about 88 per cent of the shrubs, of which only one-eighth were *A. cana*. On these two-thirds, 50 per cent of the *A. tridentata* and 97 per cent of the *A. cana* bushes were found in the fall of 1935, to be more than half killed. All the *A. cana* of the middle third, making up 70 per



FIG. 1. Powder River bottom about 30 miles east of Miles City, showing cottonwoods (*Populus sargentii*), injured and even killed by drought. Note the dead branches in the crowns of the most vigorous trees. September 8, 1935.

FIG. 2. Drought damage to *Artemisia cana* in Paddy Fay Bottom. Note the uninjured sagebrush to the left around the waterhole. The bushes on the plateau, a considerable number of which have also succumbed to drought, are principally *A. tridentata*. June 7, 1935.

cent of the stand there, and all but 5 per cent of the *A. tridentata* bushes were more than half killed.

Whether or not the dying out of the sagebrush is a result of "struggle" between the two browse species and the grassy vegetation for the possession of the ground, the result is a change of vegetative aspect, from brushland to grassland, and provides an example of climatic change altering the boundaries of consociations.

Similar changes of aspect may be observed at the junction of almost any stand of *A. tridentata* and grassland in this vicinity. The sagebrush outposts are the most severely stricken (and some whole stands of this drought-resistant species have been practically wiped out), and the result is a shrink-



FIG. 3. A plant of *Artemisia cana* from those shown in figure 2, making strong recovery after most of its crown had been killed back by drought. August 29, 1935.

ing of the frayed edges of the stand toward sites where it is able to maintain itself compactly. McIntyre and Schnur ('36) have reported a somewhat analogous change in the alteration of the composition of Pennsylvania oak forests as a result of the drought of 1930.

EFFECTS ON HERBACEOUS VEGETATION

To the stockman of southeastern Montana and communities dependent on his welfare, the damage done to shrubs and trees by the drought brought only a fraction of the distress of that done to herbaceous vegetation. Although the two species of sagebrush and some other browse species are of considerable value for winter feed, the principal range forage is grass.

Because of the unusual spring warmth in 1934, herbaceous vegetation reached its maximum development and summer dormancy began about a month earlier than in the more normal years, 1933 and 1935. The native grasses were markedly shorter in 1934 than either the year before or after. *Poa secunda* grew about two-thirds, *Agropyron smithii* and *Buchloë dactyloides* about three-fifths, and *Bouteloua gracilis* about one-third as tall as in 1933 and 1935. It was observed in 1935 that the native grass inside an enclosure, which had been watered during 1934, was decidedly more vigorous than grass which had experienced unrelieved drought. By June 26, 1935, *Bouteloua gracilis* inside was largely in head. Outside, where the full effects of the drought had been felt, a few plants were just coming into head. By July 2, the plants inside were well in anthesis, whereas those outside, which were smaller and produced relatively few, puny culms, were in several stages up to and including anthesis. Many did not head at all. Similarly, *Agropyron smithii* plants were in full bloom inside by July 2, but outside a contrastingly large proportion were shorter, less robust and mainly in preliminary stages of development. It seems evident, therefore, that the effect of a drought on plant vigor extends into the following season.

The decrease in density of the grasses was very evident by 1935. Former mats of *Bouteloua* and *Buchloë* were then mats of dead material, with surviving small tufts and sprigs of green. A more exact record is to be had from the records of square meter chart-quadrats, summarized in table II. There

TABLE II. *Changes of the principal species on 55 quadrats, under varying intensities of grazing*

Species	Number of quadrats	Total area sq. cm.		% change
		1933	1935	
<i>Bouteloua gracilis</i>	43	84,806	21,417	-75
<i>Agropyron smithii</i>	50	11,305	2,927	-74
<i>Buchloë dactyloides</i>	23	48,157	10,182	-79
<i>Carex filifolia</i>	16	2,730	2,393	-12
<i>Stipa comata</i>	30	2,278	871	-62
<i>Poa secunda</i>	48	2,333	6,501	+179
Others	55	10,984	3,102	-72

the total area in 1933 of each of the principal species is compared with that in 1935. The comparison should properly be made with 1934, but in that summer some quadrats were charted before the full effects of drought were felt, and on those charted later the vegetation was so badly dried that dead and dormant material were sometimes indistinguishable. The comparison with 1935 involves some advancement of the vegetation toward recovery, so that probably the decreases in the table are even a little conservative.

The standard errors of the decreases by quadrats of the species listed in table II were found, in spite of considerable variation in site and grazing use, to be quite small compared to the changes. Two species of cactus, *Neomammillaria missouriensis* and *Opuntia polyacantha*, show net increases, but with such

large standard errors that it would be a mistake to consider them as benefitting from the drought. It is simply that cactus on some quadrats responded differently to the drought than on others.

The decreases in table II have some correspondence to the effects of drought noted on chart quadrats by Savage and Jacobson ('35) at Hays, Kansas, who found reductions in the combined areas of grama grass, *Bouteloua gracilis*, and buffalo grass, *Buchloë dactyloides*, averaging from 44.4 to 74.8 per cent, depending on the degree of grazing use.

The outstanding exception to the general loss is *Poa secunda*. Its increase was quite noticeable even to casual observers in the spring of 1935, and from its prominence many people got the idea that drought had not damaged the range after all. But this grass flowers early and soon withers, so that an increase of it does not nearly compensate in either a phytosociological or an economic sense for the heavy losses in other species.

The increase in *Poa* was brought about not only by the expansion of established plants, but also by the establishment of many new ones. On the 12 quadrats which have been charted since 1932 and which support *Poa*, new plants were found as follows: 20 in 1933, 22 in 1934 and 110 in 1935. Practically no seedlings of other species became established in 1934.

A partial explanation for such a startling increase in area may be the *poa's* habit of growing late in the fall and early in the spring. As a rule, it reaches the flowering stage by the time the growth of *Bouteloua* and *Buchloë* is fairly begun. The spring of 1934 was early, so that although *Poa* produced few, if any, viable seed, probably it was able to complete more growth than the other species. There was sufficient fall rain the following September so that it got a good start toward its 1935 development; and in the spring of 1935, as well as in the fall of 1934, possible root competition from other species was much lessened. Such an explanation does not take account of the decrease of *Carex filifolia*, which is similar to *Poa* phenologically. However, it is only fair to note that the decrease of *Carex* is less than that of the other species.

Figure 4, a fairly typical area of nine square decimeters from a quadrat charted by the same man in 1933 and in 1935, illustrates the changes that have taken place on sandy loam soil where *Bouteloua* is dominant. All the clumps of *Bouteloua* have shrunk, and in this instance the plants of *Agropyron* have disappeared completely. The increase of *Poa* is in strong contrast.

Of the more important species, *Stipa comata* seems to be the one best able to recover from the drought. Many of the old plants were killed, but considerable numbers of seedlings, all firmly rooted, as if the seed from which they sprung had been buried very deep, were observed to be coming up in 1935. The fairly typical quadrat D-3, for example, had 31 small stipas in 1935, of which only one was a survivor of the 10 large plants that had been present in 1933.

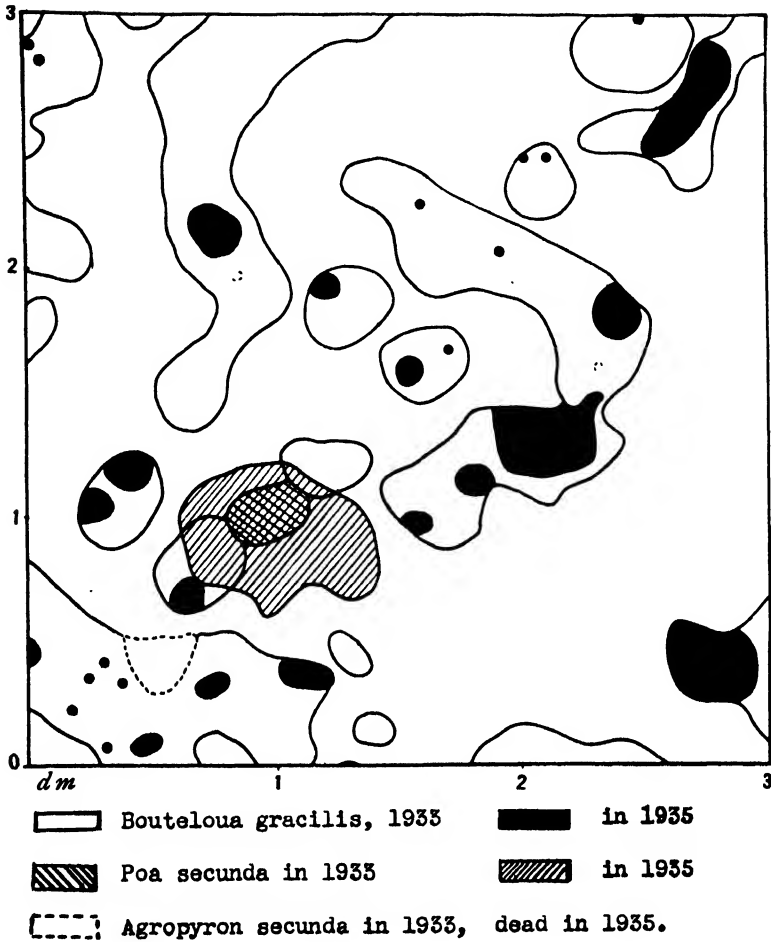


FIG. 4. A block of nine square dm. from Quadrat B-1, illustrating decrease in *Bouteloua gracilis* and *Agropyron smithii* and increase in *Poa secunda*.

SUMMARY

The extensive drought of 1934 was severely felt in southeastern Montana. U. S. Weather Bureau data for Miles City show 1934 to have been the driest year in the entire 57 years' record. Summer rainfall was only 3.53 inches, 37.9 per cent of average, and temperatures were exceptionally high. It seems likely that the effects of this dry season on the native vegetation were aggravated by the preceding series of dry years.

Injury to woody plants is to be observed near Miles City in stands of pine, juniper, cottonwood, sagebrush and other species. The 1934 diameter growth in many individuals was less than for any other year. The tops of some were partially or completely killed back, depending on the site. Some like

Artemisia cana were able to regenerate from below ground more or less successfully in 1935, but others like *Artemisia tridentata* died when the tops were killed. The result has been readjustment and redefinition of consociation boundaries in many places.

The drought, beyond stunting the herbaceous vegetation in 1934, probably affected that of the following year. Phenological observations on *Agropyron smithii* and *Bouteloua gracilis* indicate that flowering in the spring of 1935 was retarded and lessened. Injury to herbaceous vegetation, from the records of charted quadrats, was very great. The most important decreases between 1933 and 1935 were, based on the figures for 1933: *Bouteloua gracilis* 75 per cent, *Agropyron smithii* 74 per cent, *Buchloë dactyloides* 79 per cent, *Stipa comata* 62 per cent and *Carex filifolia* 12 per cent. In surprising contrast is the increase in area of *Poa secunda* of 179 per cent; and although the established plants of *Stipa comata* suffered heavy decrease from the drought, a large number of deep-rooted seedlings were observed to be coming up in 1935.

The decrease of forage is more than a one-year loss, for, as the record shows, the favorable season following the drought failed to restore the perennial vegetation to anywhere near its former condition. In the agricultural economy of the region, the likelihood of recurrent droughts and slowness of vegetative recovery are fundamental restrictions to the size of the human population. Failure to recognize them has already resulted in much loss and suffering and the abandonment of great numbers of homes. It seems fairly evident that the population, to be in ecological balance with this environment, should be no greater than can use the ranges lightly enough to permit recovery and accumulate a forage reserve against future droughts.

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CERTAIN EFFECTS OF NUMBERS PRESENT ON THE EARLY
DEVELOPMENT OF THE PURPLE SEA-URCHIN, *ARBACIA*
PUNCTULATA: A STUDY IN EXPERIMENTAL ECOLOGY

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Thirty years ago Ganong outlined accurately a modern approach to the study of physiological life histories of organisms. He included ecological relations of all stages of the life history of the organism as an integral part of its ecology. He stated the need for knowledge concerning the environmental relationships at fertilization, during cleavage and early embryonic development, as well as those that exist later in the life history. In the natural preoccupation with the opening of an almost limitless field, many ecologists have ignored ecological relations of early embryonic stages and generally have begun their studies when, as larvae or nymphs, the organisms have assumed a rôle in the community roughly comparable with that of adults of other phyla or classes, if not of their own.

The tendency to ignore the ecology of early development has been the more easy since students of general embryology and of general physiology have given considerable attention to environmental relations during these early stages of development. Sometimes the ecological implications of these studies have been recognized (*cf.* Shelford, '20; Riddle, '24); more frequently this recognition, if it existed, has remained unexpressed.

In connection with an extended exploration of the physiological, ecological and sociological effects and implications of animal aggregations (Allee, '31, '34), the senior author was attracted by the opportunity offered to study mass relations in actively developing, non-motile, and relatively easily controlled groups of eggs of the purple sea-urchin, *Arbacia punctulata*. Such developing eggs have the further advantage of being self-contained as regards food supply.

As is well known, sea-urchins shed eggs and sperm into the surrounding sea water. Fertilization is external and the organism passes rapidly through cleavage stages and forms a hollow blastula. Gastrulation soon follows; the ciliated gastrula breaks loose from its fertilization membrane and develops into a free-swimming pluteus larva which at length metamorphoses into a tiny sea-urchin. These processes, up to and including the fully developed pluteus, readily take place in the laboratory and the resulting organism may be normal in all respects. Many aspects of this development have been carefully studied and there is a rich literature on the subject.

Ill effects from over-crowding on the development of sea-urchins have long been known. For example, Vernon ('95) found that such crowding produced dwarfed individuals, a result which he attributed to the concentration of excretory products in the water. The growth of the larvae appeared to be reduced by the accumulation of their own excretions and even more so by those of adult echinoderms of the same species.

Peebles ('29) verified these findings and extended them by demonstrating that it was possible to secure a growth promoting substance which was apparently associated with the protein fraction of aqueous extracts of plutei. Frank and Kurepina ('30) reported stimulation of the rate of development associated with crowding when sea-urchin eggs of an unnamed species were allowed to develop in hanging drops. They followed development up to forty-two hours after fertilization, at which time the embryos were swimming gastrulae. Without critical experimentation, Frank and Kurepina assumed that the results were produced by the action of mitogenetic rays.

The experimental work on which the present report is based was begun by the senior author in association with Dr. J. R. Fowler at the Marine Biological Laboratory at Woods Hole during the summer of 1931. It was carried forward by the present authors in connection with work reported elsewhere in the summers of 1934 and 1936 (Allee and Evans, '34, '37a, '37b, '37c). Eggs and sperm of *Arbacia punctulata* only were used. The eggs are globular and have a diameter of 74μ (Harvey, '32). The methods were those standard for experimental embryological studies with this animal, its eggs and spermatozoa, as developed at Woods Hole and summarized by Just ('28) in so far as these were applicable to our problem. New methods developed were tested critically and have been described elsewhere.

EFFECTS OF NUMBERS ON CLEAVAGE

In determining the effects of numbers upon the rate of cleavage, two main techniques were used: (1) The time to fifty per cent cleavage was determined in closely associated and simultaneously treated dense and sparse populations for first and second cleavages, and (2) eggs were killed at intervals during first, second and third cleavages so that the difference in percentage cleaved could be determined for the killed eggs at approximately mid-cleavage for a dense population and for a series of accompanying sparsely populated cultures.

These experiments have been reported in detail elsewhere; in summary, with the first method, the mean time to fifty per cent first cleavage was 0.88 of a minute slower in sparsely populated drops of 10 or 20 cu. mm. Similarly, the sparse populations reached fifty per cent second cleavage 2.23 minutes after the accompanying densely populated drops. These means have statistical probabilities (so-called "P" values) of 0.053 and 0.0016 respectively when 0.05 is the conventional upper limit of statistical significance. The smaller the fraction in this case, the greater is the significance.

With drops of 20 cu. mm., using the second method, at approximately mid-cleavage, the sparse populations had 14, 18 and 9 per cent fewer divided at the first, second and third cleavages respectively. The corresponding statistical probabilities are 0.0001, 0.00001 and 0.022, all of which are significant.

Probably because of increased hypertonicity in the smaller volumes resulting from unavoidable evaporation, dense populations of *Arbacia* eggs cleaved more rapidly in 220 cu. mm. of sea water than did accompanying populations of equal size in 20 cu. mm. There was, however, no significant difference between the rate of cleavage of similar populations in 220 cu. mm. as compared with those in approximately 2 cc. of sea water. In both of these larger volumes, at second cleavage, the only one tested, sparse populations divided significantly slower than did accompanying dense populations just as they did in drops containing 20 cu. mm.

There is thus clear evidence that under a variety of laboratory conditions, the eggs in sparsely populated small amounts of sea water cleaved more slowly than did accompanying lots of crowded eggs when the degree of crowding is the only known controlling variable. Experiments to date have not revealed the causal mechanisms involved. Preliminary tests using a slight increase of CO₂, so-called egg-water in which unfertilized eggs have stood, or so-called cleavage water in which cleavage has taken place, have retarded rather than stimulated cleavage rate.

Under the conditions of our experiments, using drops of 20 cu. mm. housed in small moist chambers, the stimulating effect of crowding could be detected when 65-164 eggs were present in the more crowded drop and 5-24 eggs made the accompanying sparse population. There was no significant difference in rate of first or second cleavage when populations of 22-56 were compared with those of 5-18 (Allee and Evans, '37b, '37c).

LATER DEVELOPMENT

In the present paper, we wish to report certain effects of crowding upon later stages in the development of *Arbacia* and to consider the general ecological implications of the findings.

All experiments were carried on in a room with north exposure only, so that extreme temperature fluctuations were avoided. During the first cleavage stages, the temperature was lowered, if necessary, so that first cleavage came about sixty minutes and second cleavage about ninety minutes after fertilization. Thereafter the small moist chambers containing the developing eggs were placed on the work table exposed to room temperatures. Few temperature readings were taken at night; so far as observed, the room temperatures varied from 21° to 25.5° C. during the course of the experiments to be reported here. With the exception of one individual test in which double the usual volume was used, all experimental drops contained 10 cu. mm. They were protected from evaporation by sealed covers which formed small moist chambers.

Except in the experiments with hypotonic sea water (see table II) the drops containing the dense populations were set up first and hence were exposed to evaporation slightly longer than were the accompanying sparsely populated drops. The latter contained more carefully selected eggs since Allee, who did all the isolating (and who made most of the definitive observations recorded in this paper), found it psychologically difficult to pick up eggs for the sparse populations which were obviously imperfect. The dense populations were scooped up by the haemocytometer pipette-full, and with them, no such selection was possible. Thus on two counts, the experiments were weighted against the trend of experimental results.

The type of data available is suggested in summarized form in table I. This tabulation reviews the state of development 18 to 23 hours after fertilization, after the cultures had stood over night, for experiments conducted in filtered normal sea water placed in drops of 10 cu. mm. in assembled moist chambers. These latter consisted of a glass base four centimeters square. The vertical wall was formed by a glass ring about three millimeters high; it was sealed to the base with vacuum grease and a plain glass cover was sealed on with vaseline.

A series of vaseline rings of approximately equal diameter were made on the clean base of such a chamber. The central drop, which contained the dense population, was surrounded by five drops each of which held one or a very few eggs. Extra drops of sea water were often introduced in order to lessen the evaporation from the experimental drops. Soon after the initial set-up was completed, about fifteen minutes after fertilization, the whole small moist chamber was placed in a cooling device in order to control cleavage time. On being taken from this cooling chamber to determine 50 per cent first or second cleavage, the covers became clouded with moisture and had to be replaced. This increased slightly the evaporation from the contained drops. After finding 50 per cent second cleavage, the moist chamber was set aside at room temperature for inspection at about 9:00 the following morning.

Table I shows that cleavage was slightly better, on the average, in the sparsely populated drops. The following morning, however, almost half the embryos in the sparsely populated drops were dead while only three per cent of the denser populations had died. The denser population had also, on the average, developed faster than the accompanying sparse populations.

Each pair of items in table II is based on data similar to those summarized in table I. In the first two comparisons given and in a part of the last, the sparsely populated drops were in small moist chambers on separate slides. This difference in handling did not alter the results obtained. The following remarks are pertinent with regard to these greatly condensed summaries: For the first six paired comparisons which show observations made 18 to 23 hours after fertilization, there was uniformly a higher percentage of mortality in the sparse populations. The mean difference is 35.1 per cent with "P" equal

TABLE I. *Effect of numbers present on development and survival in drops of 10 mm.³ in assembled moist chambers, 18-23 hrs. after fertilization; highest average in sparse population was 4.2 individuals per drop; sparse populations italicized. Temperature after 2nd cleavage was 22-24° C.*

Numbers present	% cleavage	% dead	% early gastrula	% gastrula	% early plutei
60	84	14	0	86	0
15	87	0	100	0	0
377	78	12	0	88	0
9	89	0	25	75	0
1000±	98	15	0	0	95
22	91	0	50	50	1
1000±	96	10	0	60	30
12	100	0	0	67	33
11	91	20	50	20	10
2000±	97	2	0	0	98
7	86	100	0	0	0
2000±	94	2	0	0	98
8	100	100	0	0	0
1000±	96	2	0	98	0
7	100	100	0	0	0
1500±	97	5	0	0	95
4	100	25	25	50	0
1800	94	0	0	0	100
8	75	100	0	0	0
2500±	97	0	10	90	0
8	100	0	25	75	0
2600±	98	0	0	50	50
9	100	0	0	89	11
1200±	94	0	0	0	100
10	100	100	0	0	0
1000±	95	0	0	0	100
8	87	86	14	0	0
2000±	98	0	0	0	100
12	83	10	60	30	0
2400±	98	0	0	0	100
8	100	36	0	0	64
2500±	98	2	0	0	98
8	100	100	0	0	0
Dense	93	3.2	0.8	31.7	64.5
Sparse	95	48.6	21.8	24.3	5.3

to 0.0126. In the cultures that stood another 24 hours, this initial difference had disappeared.

Almost all the cultures had passed the early blastula stage when examined and the great majority of those in the dense populations had passed the early gastrula stage. None of the differences between dense and sparse populations in the different stages recorded in table II are statistically significant except the last where the mean difference of 37.8 per cent has a "P" value of 0.0455. There is, however, evidence of a definite trend toward more rapid development of the denser cultures. When all the available data collected 18 to 23 hours after fertilization are combined into two sets of comparisons, (a) those in early gastrula or preceding stages and (b) those in good gastrula or later stages, the respective mean differences are: (a) 20.5 and (b) 55.7 per cent with "P" values of 0.0042 and < 0.0002. Both of these differences are highly significant statistically.

TABLE II. Summarizing table of the effects of numbers present on development and survival of *Arbacia* embryonic stages. All cases were summarized at 18-23 hrs. after fertilization except the last pair of comparisons which were made after 40 or more hours following fertilization

Conditions	Population	Numbers present	Cases followed	% cleavage	% dead	% early blastula	% blastula	% early gastrula	% gastrula	% early plutei
Paraffined slides }	Dense	26-137	21	97	17	3.5	9.7	15.0	54.8	0.0
	Sparse	1-4	137	97	61	5.9	7.4	18.4	7.1	0.0
Glass slides }	Dense	35-331	24	93	19.9	0.0	6.4	13.2	38.1	22.4
	Sparse	1-2	117	95	49.2	0.0	26.2	7.2	9.5	7.9
Hanging drops }	Dense	11-343	12	95	10.9	0.0	0.0	9.3	69.8	10.0
	Sparse	1-5	59	95	13.3	0.0	8.3	25.1	52.3	0.9
Assembled moist chamber }	Dense	12-2600	17	93	3.2	0.0	0.0	0.8	31.7	64.5
	Sparse	1-8	80	95	48.6	0.0	0.0	21.8	24.3	5.3
110% sea water }	Dense	79-2000	12	97	1.8	0.0	0.0	4.2	37.2	56.8
	Sparse	1-4	59	98	62.9	0.0	13.2	17.6	4.2	2.1
90% sea water }	Dense	1500-4000	9	95	0.0	0.0	0.0	0.0	5.5	94.4
	Sparse	1-5	47	98	28.2	0.0	0.0	34.3	32.4	5.0
40 hrs. after fertilization }	Dense	53-255	8	89	52.9	0.0	0.0	0.0	15.6	16.4 ¹
	Sparse	1-4	60	91	50.4	0.0	0.0	0.0	16.6	20.0 ²

¹ Also 15.6 plutei.

² Also 13.0 plutei.

There are only a relatively few cases which have been followed for approximately another 24 hours. These indicate that the initial advantage found in the denser lots disappears and ill effects of crowding become apparent, such as have been reported frequently.

Another pertinent fact remains to be recorded: throughout the whole series, there were occasional isolated eggs that developed as rapidly as did the best of the accompanying eggs in the denser populations. During the time they were followed these isolated embryos grew as well as did the best of the accompanying dense populations. Such eggs and embryos were exceptional in our experience; the fact that they exist indicates clearly that under the conditions of our experiments, crowding was not absolutely necessary for rapid development.

CAUSAL FACTORS

Under the conditions we have been testing, not only do the crowded eggs pass first cleavage stages earlier than do those isolated or in sparsely populated drops but the early embryonic development is also speeded up and it is only some time after the first day that the well known harmful effects of overcrowding appear. Some of the essential factors in these experimental con-

ditions are: the developing eggs are cultured in small drops which provide for sufficient aeration; they must, however, be carefully protected from evaporation. The rate of respiration of newly fertilized eggs increases enormously and there is a very high rate of respiratory metabolism throughout all these early stages. The developing organisms must therefore give off large amounts of carbon dioxide. In the drops used, this could diffuse out of the water much more readily than in larger quantities of water with a lower ratio of surface to volume. Other products of metabolism which can be oxidized would, under the conditions of these experiments, have relatively ready access to oxygen.

In five experiments with a specially constructed cooling device, results from which have not been included in the preceding summaries, toxic substances of an undetermined kind are known to have been present. Under these conditions, all relatively isolated eggs were dead at 18 to 23 hours after fertilization. In some cases they did not even cleave. In one instance all those in the dense population were dead at about 18 hours after fertilization; in the other cases followed, the embryos were mainly alive and, in two experiments, had developed as far as early plutei. This is as far as any of the other populations had gone in the same length of time. This experience demonstrates again the protective action of numbers in the presence of a limited amount of toxic materials (*cf.* Allee, '31, '34). There is no indication of toxicity in any of the other experiments; there may have been some in those performed on slides coated with paraffin. Certainly there was none in the hanging-drop experiments which showed the same experimental trend as that given throughout these tests.

Suggestions concerning the presence of stimulating amounts of carbon dioxide, or of other products given off into the medium, or of locally increased temperature as a result of the mass of rapidly oxidizing protoplasm present in the crowded cultures, or of stimulation from a slight lack of oxygen, or of physical emanations such as the so-called mitogenetic rays, are easily made and the possible action of certain of them can readily be checked experimentally; with others experimentation is more difficult. In the absence of experimental analysis, speculation concerning causation seems unwarranted.

DISCUSSION

For some years, the senior author and his associates have been engaged in investigating the effects of numbers present on various biological processes. Attention has been focused more than elsewhere on the problem of possible optimum populations at some point above the minimum possible. Under certain conditions the optimal numbers coincide with the minimal populations; however, demonstrations have been made under a variety of conditions and with animals widely distributed in the animal kingdom which show that the minimal population is not necessarily optimal. The present report adds an-

other case to this record. Under the laboratory conditions tested, sea-urchin eggs develop more rapidly for at least the first 18 to 23 hours after fertilization, if somewhat or even greatly crowded in small drops of sea water than if relatively isolated. No attempt has been made to test such effects in larger volumes, except in early cleavage stages where they still hold, and the application to conditions in nature is speculative.

It seems likely that as regards aeration and consequently a relatively plentiful supply of oxygen for the rapidly developing embryos and for the oxidation of organic wastes, conditions in such drops as we have used approach those found in nature closer than do those which obtain when dense populations of developing eggs are placed in finger bowls, or in other large vessels, in which the surface-mass relations would be much reduced as compared with those of the small drops employed in the present studies.

It is known from the work of others (*e.g.* Lillie, '19) that sperm of many marine organisms, *Arbacia* among them, live longer and retain their fertilizing power longer if massed than if in sparse populations. Grave ('28) has shown that under dilutions of from 1/2000 to 1/10,000 per cent, *Arbacia* sperm survive from three to ten hours and a very few retain their fertilizing power for from twelve to twenty hours. They can swim in quiet water about thirty centimeters in about five hours but can, of course, drift much farther in currents of sea water in this time. The distance that sperm can travel and still retain fertilizing power is definitely limited; hence adult sea-urchins must be more or less closely aggregated to insure the development of progeny. There is every reason to believe that if an isolated egg of *Arbacia punctulata* were encountered by a single sperm, fertilization and development would result provided all conditions were favorable. These new data of ours indicate, however, that more rapid development, at least up to the freely swimming planktonic stages, would result if many eggs develop in a limited space than if any one or a few are present. The later retardation which we have found associated with crowding, and which has been repeatedly reported by others, is the less significant since in nature the swimming plutei in this stage of development would be scattered in part by their own efforts and more by the convection and other currents present in the waters of their natural spawning grounds.

Although the conditions of our experiments do not reproduce those in nature, there is more support than opposition in the literature for the suggestion that similar effects may exist in reproduction of sea-urchins under natural conditions. Even though the relations we have discovered should in time be found to hold under special conditions only, the fact that under these circumstances the optimal population for speedy development to swimming plutei is well above the minimal possible, appears to be significant.

Such considerations indicate, as the senior author has said elsewhere, and as Espinas among others suggested years ago, there is in nature, not only the general ecological principle of competition frequently dramatized under the

heading of the inter-individual struggle for existence but also a counter principle of unconscious co-operation or automatic mutualism which is the opposite of inter-individual struggle. This has been demonstrated experimentally in recent years to exist for many organisms under diverse conditions and mechanisms of its operation have been found in some cases. Although the fact of the working of this principle of automatic mutualism seems to be definitely proven for developing eggs of *Arbacia*, there is no indication yet of the mechanisms involved.

SUMMARY

Under the conditions of our experiments, crowded populations of eggs of the sea-urchin *Arbacia punctulata* survive better and develop more rapidly through the early cleavages and up to some 18 to 23 hours after fertilization, than do developing eggs in accompanying, sparsely populated drops. When examined a day later, these initial advantages have disappeared. The causal mechanisms are unknown. Certain ecological implications are suggested.

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BRYOXIPHIMUM NORVEGICUM, THE SWORD MOSS, AS A PREGLACIAL AND INTERGLACIAL RELIC *

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The remarkable disjunct distribution of *Bryoxiphium norvegicum* (Brid.) Mitt., as well as its varied history, gives this species uncommon interest to botanists. Its structural, and consequently systematic, isolation, and the restriction of the plant to one type of habitat add still more to the fascination of the "sword moss." The late Mrs. Elizabeth G. Britton, for many years the leading American bryologist, made the statement that her discovery of this species in a fruiting condition in the Dells of the Wisconsin River, in 1883, was responsible for the beginning of her career in bryology.

As the species was known at that time only from Ohio and Kentucky, and as the sporophytes had neither been described nor even collected previously, her discovery was of primary importance, for it enabled the taxonomic position of the plant to be determined for the first time. Although the present generic name had been given in 1869, the affiliations of *Bryoxiphium* with other genera were not known. It has been decided finally that there are no close affiliations and a family has been made for this one genus.

A curious feature of the history of *Bryoxiphium norvegicum* is that authentic material from Norway, or for that matter, from Europe, has never been seen. Desvaux sent the plant, from a source now unknown, to Bridel, under the manuscript name "*Fissidens imbricatus*." Bridel (1827) renamed and published the species as "*Phyllogonium Eustichia Norvegica*," apparently assuming that the specimen originated in Norway.

In spite of the careful work of later collectors in Scandinavia, the species has not been discovered there. The existence of *Bryoxiphium* in Iceland was discovered early in the nineteenth century, however, from the collection of Vahl, and its abundance there confirmed by a number of later collectors.

As a result, the conclusion was reached by bryologists that the Norwegian origin attributed to Desvaux's specimen was an error, and that the type material must have been collected in Iceland. This belief was apparently first voiced by Sullivant (1856), who, in speaking of the North American distribution, said: "The only other certain habitat for this very interesting Moss is Iceland. That of Norway is apparently a mistake." The same idea is echoed by Mönkemeyer ('27), who says: "Trotz des Beinamens "*nor-*

* Papers from the Department of Botany and the Herbarium of the University of Michigan, No. 594.

vegicum” ist dieses aus Nordamerika bekannte Moos vom europäischen Festlande nicht nachgewiesen. Erst durch A. Hesselbo wurde es auf seinen Reisen (1909, 1912 und 1914) von Island auf Lavablöcken bekannt.” The last remark is an obvious error, difficult to understand in view of the many early reports of *Bryoxiphium* from Iceland, and the account in the *Bryologia Europaea*.

Bryoxiphium norvegicum was first discovered in North America by Sullivant, who distributed it from Columbus, Ohio, before publishing the report of his discovery. Evidence of this is given by a specimen in the Herbarium of the New York Botanical Garden with the data: “Wet overhanging rocks, Columbus, Ohio, Mr. Sullivant, 1841.” That the species was not actually found at Columbus, but only distributed from Sullivant’s home there is shown by the fact that the labels of the specimens issued four years later (Sullivant, 1845) bear the legend: “Hab. in collibus rupestribus umbrosis circa Lancaster, Ohionis.” The first report of the discovery which was really published and which had wide circulation seems to be when the tickets of the Musci Alleghanienses were reprinted in the form of a small book (Sullivant, 1846a), for more general distribution. Only about fifty sets of the actual specimens were prepared, for presentation rather than for sale. The same year, Sullivant (1846b) published a very complete study on *Bryoxiphium*, and gave more explicit information concerning its habitat. He explains that the specimens came from “the perpendicular faces of sandstone rocks, in moist shady places, six or eight miles south of Lancaster, Ohio.”

Bryoxiphium was again distributed in 1856, as No. 109, in Musci Boreali Americani, issued by Sullivant and Lesquereux. The general distribution then known is still given on the label as southern Ohio. In the so-called second edition of this work, in 1865, under the same title, but with very little duplication of the species of the first edition, we find the range stated as follows: “Hab. ad rupes arenaceas in umbrosis et humidis Ohionis inferioris; etiam in Kentucky meridionali.”

The known distribution of *Bryoxiphium* was still restricted to lower Ohio and southern Kentucky when Mrs. Britton (Knight, 1883) made her noteworthy discovery of fertile specimens in Wisconsin, but was soon extended to Ferns, in Putnam County, Indiana, by L. M. Underwood (1891), and to Lamoille Cave, in Winona County, Minnesota, by J. M. Holzinger (1894). Since the turn of the century and the revival of interest in bryophytes, *Bryoxiphium* has been recollected many times at the old localities, and several new stations have been discovered.

Through the kindness of several correspondents (especially G. W. Blaydes, W. H. Camp, and Winona H. Welch), as well as an examination of the Herbarium of the New York Botanical Garden, and a search of the literature to date, the known distribution of *Bryoxiphium norvegicum* has been compiled.

Iceland: Krisuvik; Thingvellir; Glacier originating from the Jökul; Kilvidarhol; Flokastadagil; Barkarstadr; Drángshlid (Hesselbo, '18).

Greenland: Near Norwegian Radio Station at Myggbukta, northeast Greenland, 73° 29' N. Lat., 21° 34' W. Long., collected by *Sigurd Aandstad*, July 25, 1932 (Breien, '34).

Minnesota: Entrance to Indian Inscription Cave below Lamoille, Winona County, *J. M. Holzinger*, October, 1893 and August, 1894 (Holzinger, 1895).

Wisconsin: Dells of the Wisconsin River, *Elizabeth G. Knight*, July 8th, 1883 (with fruit); Banks of the Wisconsin River, near boat landing, Kilbourne City, *E. G. Knight*, July 7, 1883; Valley of the Wisconsin River near Kilbourne City, *L. S. Cheney*, July, 1894 (with fruit); Coldwater Canyon, Witches' Gulch, and Limestone Canyon, all in the Dells of the Wisconsin River, *A. M. Taylor*, June 3, 1917.

Indiana: Turkey Run, Parke County, *Lucy Allen*, August 1, 1907; *A. M. Taylor*, July 5, 1917; *G. W. Blaydes* ('27), April 8, 1927; Fern Cliffs, Putnam County, *L. M. Underwood*, October and November, 1891; *Winona H. Welch*, May, 1935.

Ohio: Near Lancaster, *W. S. Sullivant*, 1845. Dr. *G. W. Blaydes* of the Ohio State University says (personal communication): "I have collected it in Hocking County, Ohio, at Old Man's Cave, Ash Cave and Cantwell Cliffs State Parks. It occurs at these places in abundance. Also in Fairfield County, Ohio, near Sugar Grove. I have also collected it in Licking County, Ohio, near Falsburg along Wakatomika Creek."

Pennsylvania: Slippery Rock Creek, Lawrence County, *L. Lesquereux*.

Missouri: Ste. Genevieve County, *J. A. Steyermark*, January, 1934 (Steyermark, '34).

Kentucky: "In a small tributary of the Cumberland River immediately below Cumberland Falls," *A. J. Sharp*, August, 1930 (Sharp, '30). Dr. *Blaydes* says (personal communication) that *Mr. R. T. Wareham*, of the Ohio State University, has collected this species at Natural Bridge, Kentucky.

Tennessee: "Along the moist cliffs of Clear Fork Creek," near Rugby, *A. J. Sharp*, August, 1930 (Sharp, '30).

Washington: Crevices on underside of rocks, Alta Vista, Paradise Valley, Mt. Rainier, *A. S. Foster*, August, 1909.

Material from Japan and Korea, although probably very close to and perhaps indistinguishable from *B. norvegicum* is called *B. savatieri* (Husn.) Mitt. Mexican specimens are apparently distinct from *B. norvegicum* and are called *B. mexicanum* Besch.

Perhaps the most unexpected report is that of *Müller* ('01) in which he speaks twice of specimens from "Irland," which is obviously a lapsus for "Island."

The geographic distribution, because of its remarkable nature, has provided material for a good deal of speculation. *Mrs. Britton* (1897) stated the problem very well, although making no attempt to settle it. She says: "How they [the species of *Bryoxiphium*] came to be scattered in such diverse quarters of the globe as Iceland, the United States, Mexico and Japan

still remains a mystery, as well as the fact that in spite of producing an abundance of reproductive organs they still fruit so rarely."

The restriction of the species to moist, shaded, sandstone cliffs and blocks in the United States has given rise to the idea that the habitat and environment are the limiting factors in distribution, and that perhaps even the geological age of the sandstone substratum is of importance. In nearly all the recent reports of *Bryoxiphium* in the United States the geological horizon is named, and several botanists have pointed out the similarity of the ages of the sandstone exposures. In the words of Steyermark ('34): "It is worthy of mention that this moss should be found on the Lamotte sandstone in Missouri, because in Wisconsin where it occurs in greatest abundance, as far as known records are concerned, it is found, as in the Dells of the Wisconsin River, on the Potsdam sandstone; the latter, like the Lamotte sandstone, is of Cambrian age, and geologically the two sandstones are closely related in history and origin."

When all the records are examined together, however, it is seen that there is no real correlation of any significance in the horizons of the sandstones which support *Bryoxiphium*. Although those in the Mississippi basin are consistently Cambrian, the ones farther east are of Mississippian or Pennsylvanian age. Furthermore, in Iceland the species is exceedingly abundant, but grows there almost exclusively on consolidated volcanic ash, or tuff, and more rarely on lava.

Edaphic factors are apparently of some significance, however, and it will be noticed that the substratum is always one which is porous enough to hold water. Concerning the substratum in Iceland, Hesselbo ('18) says: "Tuff consists of consolidated fine-grained material (volcanic ash and dust), through which are scattered larger and smaller blocks of rock. While the basalt has a smooth surface, with fissures and depressions only here and there, the surface of the tuff is uneven and rough, and therefore offers more favourable conditions to the mosses for attaching themselves to it. When a basalt and a tuff surface occur side by side, as is often the case, the difference is very obvious. Mosses grow more scantily on basalt . . . while tuff surfaces are often covered with a continuous moss-carpet, composed of many different species." I believe that the preference of tuff to basalt by mosses may be a matter of water supply rather than texture of surface.

Bryoxiphium is apparently a calciphobe, so that the acidity of the substratum may possibly be an important factor. It is curious that nearly all the studies on the relation of hydrogen ion concentration to the distribution of bryophytes have been made on the common species which obviously have much tolerance, some of them inhabiting many different types of habitats and even different climates. It would perhaps be of more interest to study some of the rarer types which are restricted to an exceedingly static environment and which are unable to invade any other habitat.

Bryoxiphium norvegicum is an old species. It is, to judge from its present distribution, undoubtedly a member of a once widespread flora which extended over the northern hemisphere in late Cretaceous or early Tertiary times. The great uniformity of appearance and lack of variation within each species are also marks of old groups. One is reminded here of some of the conservative and unchanging phanerogams, as *Ginkgo*, *Sequoia*, or *Liriodendron*, which may be contemporary in geological age with this moss. The fossil distribution of the tulip tree resembles the present distribution of *Bryoxiphium*, and the two may be members of the same flora.

As a result of the almost complete extinction of this ancient flora, and the resultant disjunction in the present distribution of the species, it is difficult to classify it floristically. Herzog ('26) has given the only formal geographical treatment of the species, but comes to no definite conclusion. He stresses the disjunct distribution but attempts no explanation of it. On p. 233 he says: "Interessant ist das massige Auftreten von *Bryoxiphium norvegicum*, einer disjunkt nordischen Art, auf Island." Later on, in the same work, he (p. 293) includes this species in a list of those which he considers endemic to the eastern hardwood forest of the United States, with the parenthetical explanation "Sonst nur auf Island." This treatment hardly clarifies matters, as it is difficult to conceive of a plant being a member of two floras as different as the boreal flora of Iceland and that characteristic of the northern Alleghanian region. The explanation seems to rest in the age of the species, and the fact that it is a relic of an epoch with a much more equable climate.

Examination of a map (fig. 1) of the distribution of *Bryoxiphium* (in a series of such maps which are being prepared for all the North American species of Bryophytes) indicated that there is a significant similarity between the distribution of this species and that of many preglacial and interglacial relic species of vascular plants. From a considerable literature on this subject, I need to cite only the important work of Fernald ('25, '35). With the idea of preglacial relics in mind, all the reports were carefully rechecked, and it was found that each of the known specimens of *Bryoxiphium* had come from a locality which had either certainly escaped at least the Wisconsin glaciation, or for which there is good evidence that it had. Perhaps the most remarkable feature of the distribution is the restriction of a significant number of the recorded stations to the immediate vicinity of the glacial margin, and just below it.

To pass in review all the records is perhaps not necessary. The greater number of localities reported for *Bryoxiphium* need some discussion, however, and evidence will be presented to show that each one was not glaciated, at least during the Wisconsin invasion.

Unfortunately, the true origin of Desvaux's original specimen will probably never be discovered, although there is some chance that it came from Iceland (or even North America). By far the best discussion of the distribution of this moss in Iceland is that of Hesselbo ('18), who reports it from

seven stations as the result of his work and that of previous collectors. After reading his fascinating report, and examining his photographs, one can have little doubt that *Bryoxiphium* is one of the representative mosses of southern Iceland, on the vertical or overhanging sides of blocks and in ravines.

In view of the fact that Iceland is commonly considered to have been completely covered with a continental glacier, even during the last stages of the Pleistocene, it will seem foolhardy, perhaps, to see no other explanation for the presence of *Bryoxiphium norvegicum* in Iceland than its persistence there

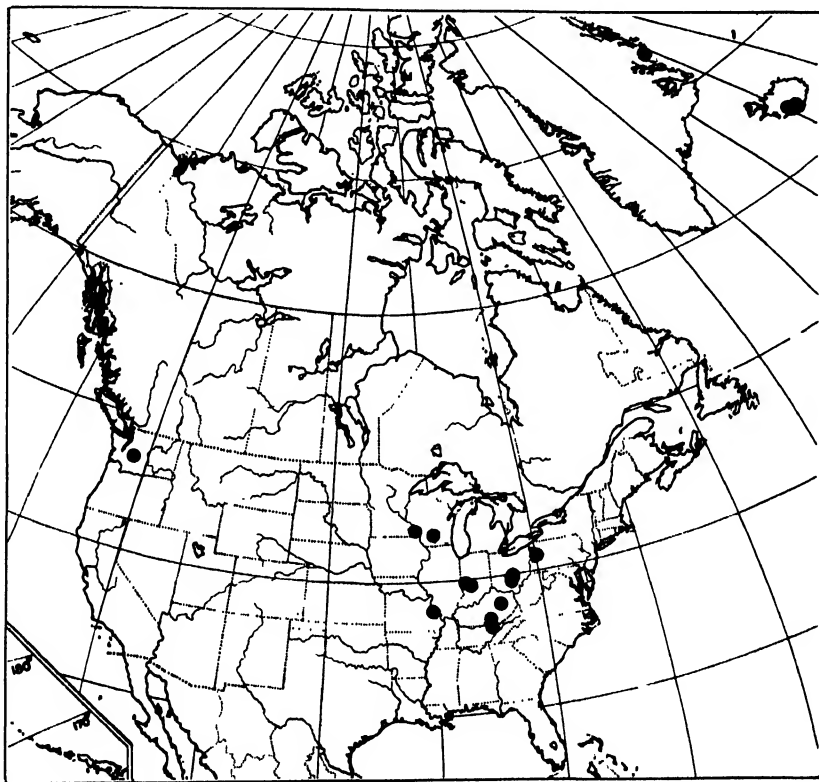


FIG. 1. The distribution of *Bryoxiphium norvegicum*.

as a preglacial or interglacial relic. However, during the last few years the idea that parts of southern Iceland escaped Pleistocene glaciation, or at least the last stage of the Pleistocene, has gradually gained weight. Lindroth ('31) says: "Und was für eine Art von Isolierung hierbei in Frage kommen kann, darüber kann wohl kein Zweifel obwalten: Ein Teil des südöstlichen Island soll nämlich während der grossen Vereisung-- jedenfalls während der letzten --eisfrei geblieben sein." (Italics his.) Later on in the same work, he says (p. 565): "Ein postglaziale Fauna-einwanderung aus Europa ist für die

ganz fauna nicht denkbar. Jedenfalls hat Island postglazial nicht mit irgend einem anderen Gebiete in fester Landverbindung gestanden. . . . Die Letzte Vereisung haben die interglazial eingewanderten Formen—soweit sie nicht wieder ausgestorben sind—auf einem eisfreien Küstenstreifen der Insel überlebt. Geomorphologische Tatsachen sowie vor allem das deutliche Hervortreten zweier getrennter Faunazentren—besonders in der Verbreitung der Coleopteren merkbar—weisen unverkennbar darauf hin, dass dieses Überwintern in Süden und Südosten stattgefunden habe, und zwar wahrscheinlich in zwei voneinander isolierten Gebieten: einerseits unter den Randgipfeln des Vatnajökulls, am ehesten in seinem österlichsten Teil in der Nähe von Hornafjördour, andererseits aber auch in äussersten Süden unterhalb des Mýrdalsjökulls oder dessen westlichen Abschnittes, des sog. Eyjafjallajökulls." It is very interesting to notice, and it is probably more than a coincidence, that the last locality which Lindroth gives as a possible haven for insects during the last ice age is very close to one of the stations for *Bryoxiphium* given by Hesselbo (Eyjafjalla).

The idea that parts of Iceland escaped glaciation is given further support by Gelting ('34) who says: "The logical conclusion may be drawn from the map on p. 269 that in Iceland, too, there must have been unglaciated areas during that period. In fact, the areas of certain Icelandic species suggest this. As such a presumed ice-free area I may mention the area around Ø Fjord. The landscape here is distinctly alpine, and a larger number of species occur which have not otherwise been found in Iceland, and the continental, Greenlandish, presumed relict species also show a relatively maximum occurrence here."

There is even more evidence to be brought up in favor of the unglaciated nature of the Greenland station for *Bryoxiphium* than for the stations in Iceland. Several parts of Greenland have been recognized, even from the beginning of scientific observation there, to be unglaciated, and it is being discovered, each year, that more and more of the coastal margin of the island has not been ice-covered. Here again, the paper which gives the best review of the literature on this subject and which presents the best case in its favor (Gelting, '34), takes up the very part of Greenland from which *Bryoxiphium* has been reported. Breien ('34) reported it from 73° 29' N. Lat. and Gelting treats the coast between 73° 15' and 76° 20' N. Lat. Gelting says (p. 251): ". . . if one studies the Greenland plants and their sometimes very peculiar occurrence in enclaves, the idea of the interglacial survivors suggests itself with a force that carries conviction." He continues (p. 269): "The centric species do not form an ecological unit, but widely different demands are represented. I take this as a proof that the unglaciated areas were rather extensive and existed for long periods. They cannot have been nunataks, where only isolated tops rise above the ice, as in the Marianne Nunataks of the present day, for the number of species on these nunataks is too small and the flora too xerophilous for this. As, further, several of the centric species are

preferably lowland-plants, or at all events show a distinct and rapid decrease in frequency up the mountains, they become an argument for the existence of unglaciated lowlands during the Ice-Age. [Italics his.] Finally the bi-centricity of *Carex ursina*, a really halophilous strand plant, makes probable the existence of unglaciated shores during the Ice-Age."

Gelting's conviction that rather extensive parts of coastal Greenland escaped glaciation is substantiated by many other workers who have drawn their conclusions from geologic-glaciological evidence, rather than that given by plant or animal distribution. An interesting summary of these works is given by Gelting.

The reports of *Bryoxiphium* from Minnesota and Wisconsin are from areas in the best known so-called driftless area, which, although glaciated in the earliest Pleistocene, escaped the Kansan ice sheet, and has certainly not been glaciated since then. The curious localization of the moss at the old ice border is marked here as elsewhere. The stations at and near Kilbourne City, and other parts of the Dells of the Wisconsin River, come very close to the westernmost border of the Wisconsin drift in this part of the State (Bean, '28). The same is true of Dr. Holzinger's record from Lamoille Cave, Minnesota. This is twelve miles below Winona, which brings one almost exactly to the margin of Wisconsin glaciation (Chamberlain and Salisbury, 1885). The only Pennsylvania record with which I am familiar is that of Lesquereux from Slippery Rock Creek, which is just south of the glacial margin, but very close to it. The same consistency occurs in Ohio, where the moss is abundant in Hocking, Fairfield, and Licking Counties, through all of which the margin of glaciation passes! Sullivant was apparently familiar with two or more localities in Fairfield County "six or eight miles south of Lancaster" (just south of the glacial boundary), although he distributed material first as from Columbus and later as from Lancaster, both of which are within the Wisconsin drift. This is relative exactitude, however, as many of Sullivant's immediate predecessors and contemporaries distributed specimens with only such data as "Rocky Mountains" or even "North America."

The Indiana localities are both well within the Illinoian drift, but very close to the line of the ancient Wisconsin ice margin. These stations show as well as any that it was the Wisconsin rather than the Illinoian ice sheet that has had so much influence on the distribution of *Bryoxiphium*. I am very grateful to Dr. C. A. Malott of Indiana University for marking the most recent interpretation of the Wisconsin glacial boundary in Indiana, on one of the maps is his scholarly paper on the glacial boundaries in Indiana ('26). This boundary, as well as the older one of Leverett ('15), shows that the Wisconsin glacial boundary runs through both Parke and Putnam Counties, which contain the only stations in Indiana for *Bryoxiphium*. Professor Malott says (in a personal communication): "The 'Ferncliff' locality is an exposure of the massive Mansfield sandstone of Pennsylvanian age which

lies within the Illinoian drift plain where it is well developed, and it does not appear at all possible that the locality escaped the Illinoian glaciation. *The locality is just beyond the limits of the Wisconsin boundary, however*" (italics mine). Dr. Malott considers the Turkey Run locality in Parke County to be *within* the Wisconsin boundary, and that the cliffs were uncovered in early postglacial times. It seems to me that the presence there of *Bryoxiphium* may, with some justice, be taken to indicate that at least a small part of the area must have been exposed during the Wisconsin stage. Far more precarious speculations have been made on the basis of much less convincing and less well known plant distribution. The Missouri locality for *Bryoxiphium*, in Ste. Genevieve County, may be interpreted in either of two ways. In the first place, it agrees with many of the preceding stations in that it is significantly close to the ice margin, as between this county and the glacial border are only small parts of the adjacent counties in Illinois, across the Mississippi River. In the second place, it is far enough from the ice border of the Wisconsin Stage to show that perhaps here in the southeastern Ozarkian highland, *Bryoxiphium* had a southward distribution during the Wisconsin refrigeration, just as in the Alleghanian highlands farther east. There is a strong possibility that the communities in the Alleghanies and Ozarks are relics. At any rate, it may be expected farther south in the Ozark uplands. The earliest record from Kentucky is apparently the notation on the ticket of No. 163 of Sullivant and Lesquereux's *Musci Boreali Americani* (1865): ". . . etiam in Kentucky meridionali." I have been unable to find any reference to the exact place where this specimen originated. Later reports from Cumberland Falls and Natural Bridge, Kentucky, have already been cited. The southernmost station for *Bryoxiphium* in the Alleghanies (and in the United States) is apparently that near Rugby, Tennessee, reported by Sharp in '31 (*l. c.*). The specimen from Mount Rainier, Washington, represents the first record for any of the western states, and is consequently important.

During the Sangamon interglacial stage, which preceded the invasion of the Wisconsin ice sheet, *Bryoxiphium norvegicum* must have had a wide distribution over northern North America, although it may have been already crowded into smaller areas by previous continental glaciations. The moss evidently exists now only where it managed to find haven. In the many centuries which have passed, it has shown no ability to reinvade old territories, or else it cannot compete against the aggressive species which have colonized the glaciated areas. The Wisconsin drift covers with a generally highly calcareous soil the habitats that were anciently available for calciphobe species. The length of time during which the moss must have inhabited the places in which it is now found is so enormous as to be almost unbelievable. Exactly the same situation has been cited many times for phanerogams and pteridophytes by Fernald, however, and an exceedingly long habitation of certain places by colonies of flowering plants which increase not at all or only slightly is rather well established.

Nichols ('16) has presented a good case for the holding over of plants from another climate in rock ravines. He says (p. 237): "Ravines in glacial till and outwash have been developed since the retreat of the glaciers, and may even now be observed in the process of active formation. In most rock ravines, on the other hand, the topographic changes since the ice age have been practically negligible . . ." (p. 244) "Many of the bryophytes . . . largely restricted to rock ravines in Connecticut, are much more generally distributed farther north. Moreover, in Connecticut, many vascular plants characteristic of the north woods, while by no means confined to this sort of habitat, attain their optimum development in rock ravines . . ." (p. 245) "On the whole, the display of Canadian plants in rock ravines is noticeably richer than in any other sort of habitat, with the exception of bogs. Various explanations for this fact may be suggested. In the first place, the atmospheric conditions here are congenial to northern plants. As compared with less protected habitats, the air is more humid, while, especially in summer, the temperature is uniformly lower and less subject to extremes. Moreover, the length of the growing season is presumably shorter than in more open situations. In a Connecticut rock ravine there may thus be reproduced in miniature a type of climate similar to that which in the Canadian zone prevails over vast areas. In the second place, geological factors are of undoubted significance. As has already been remarked, most rock ravines have remained practically unaltered since glacial times; they represent very ancient plant habitats. It seems probable, therefore, that boreal plants which today are confined to rock ravines may formerly have been much more widely distributed, and that they have been able to persist in their present habitats because of the unusually favorable environmental conditions there afforded. In the same way it is conceivable that the present boreal aspect of the vegetation in rock ravines may be reminiscent of a one-time much more universal aspect of vegetation in this region." Of course, this likewise holds true in areas that have escaped glaciation.

Attention has not been called in this country to the persistence of mosses in unglaciated areas. These areas must certainly have as distinctive species of bryophytes as of phanerogams. The only reference in the literature on American bryophytes which shows the difference in the bryophyte floras of glaciated and unglaciated areas is that of Bartram ('28), who says: "The limestone areas of the northwest coast [of Newfoundland] bordering the Straits of Belle Isle were naturally the most productive of especially interesting arctic types such as *Distichium hagenii*, *Dicranum elongatum*, *Dicranum groenlandicum*, *Desmatodon systylius*, *Stegonia latifolia*, *Bryum longii*, etc., while the southern sections of the Island are represented by more familiar Canadian types including *Dicranum majus*, *Dicranella cerviculata*, *Mnium hornum*, *Ulotia ludwigii*, *Ulotia phyllantha*, *Pogonatum capillare*, etc. . . . It seems highly probable that the calcareous forelands of the northwestern coast will amply reward further bryological activities in that region." Fernald has

found a similar difference between the phanerogamic floras of the two areas, and interprets it very logically and convincingly on the basis of a lack of glaciation in the northwestern part.

The investigation of the bryophyte floras of the various unglaciated areas, as such and for their own sake, will most certainly bring forth some entirely unsuspected and anomalous species distributions, which will have to be explained on the same basis as the distribution of *Bryoxiphium*. Many of the puzzling records of disjunct distribution of bryophytes in North America will probably resolve themselves very neatly in the same manner. It is obvious that the bryophyte flora of any unglaciated area will contain representatives of at least three main groups. (1) The majority of species are ubiquitous and aggressive ones, many of which have probably migrated into the area in postglacial times, or have lived there in spite of the surrounding refrigeration, and immediately extended their ranges in postglacial times. The presence of this large group of very tolerant species tends to obscure the presence of more significant ones. (2) Relic species of the warmer climate which existed before glaciation. These have nearly all been exterminated, apparently, although special search may reveal many more than have been suspected. (3) Boreal relics, which invaded the area as they retreated before an advancing ice sheet. These boreal relics are often conspicuous, and consequently have aroused some comment. The mixture of boreal and southern types has been reported from Pine Hollow, in Dubuque County, Iowa, which is situated within the "driftless area." Conard ('32) says: "We have recently given a complete list of all the mosses known from the area. This complete list is a curious mixture of northern and southern forms. But on the whole, the facies is that of a boreal community." Conard does not interpret the history of this interesting situation in terms of the lack of glaciation of the area, but simply compares the flora of Pine Hollow with that of northern Michigan (including Isle Royale) and northern Wisconsin. No mention is made of the fact that this part of Dubuque County escaped glaciation, hence offered refuge for many species.

Unfortunately our knowledge of the *exact* distribution of bryophytes in North America is very slight. The mosses and hepatics of the best known driftless area are so inadequately known that only a few examples of preglacial relic species can be identified. *Asterella saccata* (Wahlenb.) Evans which is widely distributed on the west coast and in the Rocky Mountains, has also been reported from one station in the unglaciated area of Minnesota, and is apparently such a relic species.

It is quite safe to predict the extension of the known range of *Bryoxiphium* to Illinois and Iowa in the next few years, as much or more on the basis of the present distribution and the presence in those states of suitable habitats, as on the basis of the lack of glaciation there. The four north-eastern counties of Iowa (Jackson, Dubuque, Clayton, and Allamakee) are in whole or in part unglaciated, and in addition are provided with moist, shaded,

sandstone cliffs and ravines. According to a map very kindly marked for me by Dr. Leighton, State Geologist of Illinois, there are three areas in the State which are considered as unglaciated. The first is a part of "the" driftless area which covers parts of three other states, Iowa, as just mentioned, Minnesota, and especially Wisconsin. This area includes most of Jo Daviess County and the northwestern corner of Carroll County. Here, suitable habitats are present. The second area is more localized, comprising the westernmost edges of Monroe and Randolph Counties. *Bryoxiphium* will probably be discovered here, as it has been found across the Mississippi River in adjacent Ste. Genevieve County, Missouri. The southernmost two or three tiers of counties in the State are also completely unglaciated, and if the proper habitats exist there, the species should certainly be discovered. Much of the state was not invaded by the Wisconsin ice sheet, and so there are many other possibilities. *Bryoxiphium* will undoubtedly be found farther south and west in the Ozarks and also in more stations in the Alleghanies.

It takes more courage, however, to predict the existence and eventual discovery of *Bryoxiphium* in other areas less well known to be unglaciated, as northern Cape Breton, the Long Range of Newfoundland, the Shickshocks of the Gaspé Peninsula, or even perhaps the Keweenaw Peninsula of Michigan.

Wherever *Bryoxiphium norvegicum* occurs, its habitat appears to have escaped at least the Wisconsin glaciation. Consequently, this species may be viewed as a helpful indicator in floristic research.

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DEVELOPMENT OF STREAM BOTTOM COMMUNITIES IN ILLINOIS¹

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INTRODUCTION

Peterson ('11, '14) and Ekman ('11, '15) paved the way for the quantitative study of aquatic communities by the invention of instruments for securing samples of known size from the bottom. Work on freshwater has ordinarily been carried on primarily with reference to pollution, or to the relation of the bottom fauna to fisheries (Adamstone, '23, '24a, '24b; Baker, '16, '18, '22, '24, '26; Coker, '29; Forbes and Richardson, '13, '19; Richardson, '21a, '21b, '25a, '25b, '29; Wiebe, '27; Thienemann, '12, '13, '21; Ellis, '31). Lakes seem to have attracted more attention than streams (Lundbeck, '26; Rawson, '28, '30; Eggleton '31; Cronk, '32).

The development of communities in areas denuded of life has interested many scientific investigators. Many studies have been made of land communities concerned only with plants. In the last decade Smith ('28), Shackleford ('29), and Bird ('30), have investigated land animal communities but the development of freshwater communities has been largely neglected. There are however, a few papers dealing for the most part with development of micro-communities in freshwater cultures (Eddy, '28; Woodruff, '12). The development of plankton communities has also been recently studied (Eddy, '34). There is also a number of descriptive papers on the fauna of streams. Many of these relate to streams which are located in the highlands of Central and Northern Europe (Steinmann, '07; Thienemann, '12, '13, '21), so are not comparable directly with those in the northern United States. More nearly comparable studies have been made by Carpenter ('27), and Percival and Whitehead ('29) on the bottom fauna of the streams of Cardiganshire, and of the rivers Aire, Nidd, and Wharfe in the West Riding of Yorkshire and by Ricker ('34) on the streams of Ontario. Investigation of the Volga River has also given information on the distribution of bottom animals (Behning, '28).

The present study of the small streams of the Sangamon River drainage system and of large artificial pools in Central Illinois streams was initiated because practically nothing was known concerning the development or rank of the communities of streams. It is largely limited to the assemblages of the stream bottom. The work has been handicapped to some degree by lack of

¹ Contributions from the Zoological Laboratory of the University of Illinois; No. 505.

knowledge regarding the life histories of some important species. For that reason it has been impossible to make specific identifications of many of the animals.

The terms for community concepts used in this paper are essentially the same as those used by Smith ('28), and Shelford ('26, '32). The term prevalent is used in the sense of predominant (Smith, '28). Prevalents are abundant or conspicuous animals which give aspect to the community throughout the year or the entire season, or are effective in changing the appearance of a habitat, or are known to have an important temporary or permanent effect upon either habitat or community. The terms faciation and facies are applied to those variations of a community of associational or associates rank characterized by the loss or addition of one or more important species (usually less than half).

The writer expresses his appreciation of the advice and suggestions given him from time to time during the course of this work by Dr. V. E. Shelford of the University of Illinois. The following men aided in the identification of the animals found, and their help is here gratefully acknowledged: Dr. H. J. Van Cleave, University of Illinois (Annelida), Mr. F. C. Baker, University of Illinois (Mollusca), Mr. R. E. Richardson, Illinois State Natural History Survey (general collection in the earlier work), Mr. B. Ellwood Montgomery, Purdue University (Odonata), Dr. O. A. Johanssen, Cornell University (Chironomidae), and Dr. Samuel Eddy University of Minnesota, who examined a portion of the bottom detritus. Through the courtesy of Dr. D. H. Thompson the map of Lake Vermillion, Lake Bloomington, and Twin Lakes were obtained from the Illinois State Natural History Survey. Several associates have given help and encouragement from time to time.

METHODS

To clarify a problem of this type, Shelford and Eddy ('29) have raised the following questions in regard to aquatic communities:

"(1) Do plants and animals gradually occupy stream bottoms denuded by floods or otherwise, until a fairly definite assemblage is attained? (2) Is the presence of some organisms necessary for the invasion of an area by other animals? (3) Do some organisms render conditions more suitable for other organisms than for themselves thus producing succession? (4) Do developing communities reach a stable condition if the changes suggested above cease to take place? (5) What are the ranks of communities studied and how many major communities occur? (6) Are freshwater communities composed of two classes of species representing an abundance or conspicuousness of individuals, first those which are widely distributed; and second those which cover only a small part of the area covered by the first. (See letter diagram, Shelford and Towler, '25.)"

Quantitative samples of the bottom inhabitants of quasi-experimental conditions represented by artificial pools and by streams of Central Illinois were made with the Peterson bottom sampler, and a triangular dredge. The bot-

tom material secured by these instruments was washed through sieves measuring forty meshes to the inch. The animals were preserved in alcohol and later counted in the laboratory. The square meter was the unit used in statistics. One-fourth to one-half of a square meter sample was considered

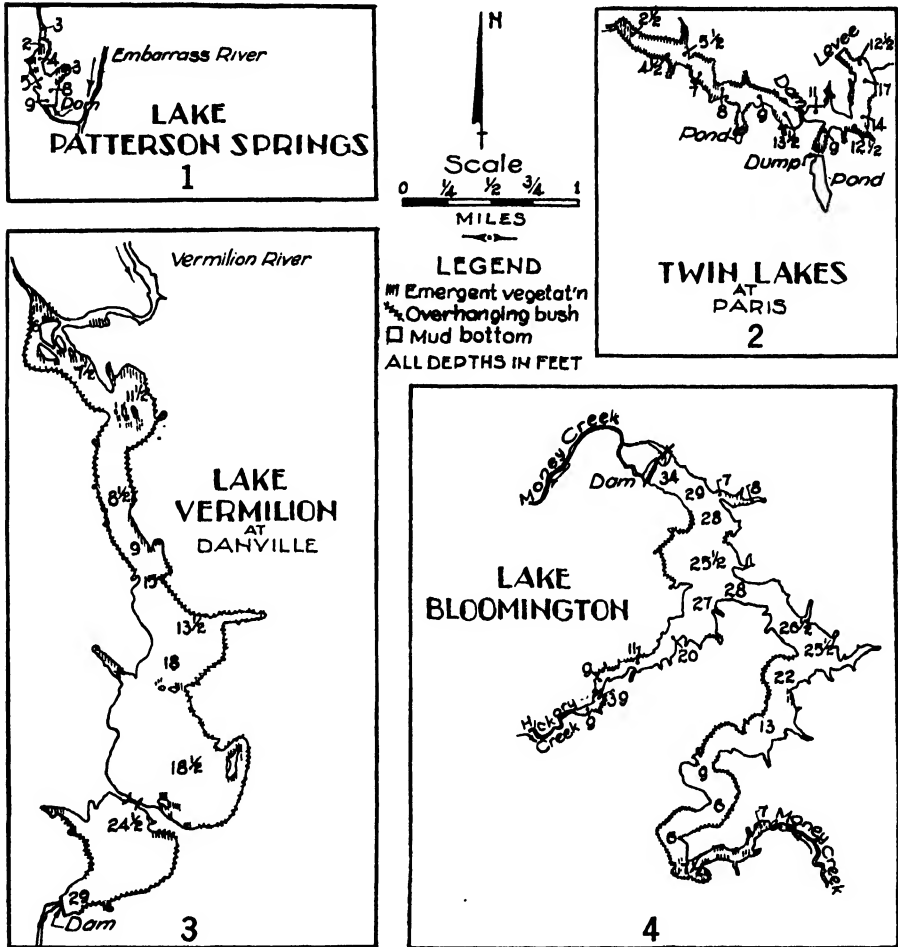


FIG. 1. Patterson Springs Lake, Camargo, Illinois.

FIG. 2. Twin Lakes, Paris, Illinois.

FIG. 3. Lake Vermillion, Danville, Illinois.

FIG. 4. Lake Bloomington, Bloomington, Illinois.

qualitatively and quantitatively representative of most of the stations. This required from four to eight samples of $\frac{1}{16}$ to $\frac{1}{14}$ square meter scattered over ten square meters.

In order to obtain the microscopic life of the stream floor, quantitative collections were made with a tube sampler. This type of instrument was first

mentioned by Peterson in 1911 in connection with his studies of the food of fishes in Danish waters. It consists essentially of a glass tube and a weight so arranged that the heavy weight pushes the tube into the mud of the stream floor. The tube measured 12 mm. in diameter. When lowered into the bottom, the mud was forced up into the tube, and adhered to the sides. After a cork was inserted into the bottom of the tube to prevent the mud from falling out, it could be readily studied. As a result of this type of sampling the various layers were measured as they occurred on the bottom. The top layer (dust—fine detritus of many writers) was pipetted off and preserved for microscopic study. Since the thickness of the detritus layer could be measured, and the diameter of the tube was known, a quantitative computation of the micro-organisms of the bottom is possible. Temperatures were taken and dissolved oxygen determinations of samples from the lake bottom were made by the Winkler method (Birge and Juday, '11). Hydrogen-ion concentration (Shelford, '23) was read with Hyson, Westcott, and Dunning indicators, and standards.

HABITATS

Quasi-experimental Pools

Towns located near unpolluted streams frequently build dams and impound water in pools of varying sizes and depths for municipal supplies. Several of these bodies of impounded water, the age of which is definitely known occur in Central Illinois. Table I gives in condensed form the description of some of the impounded bodies of water under discussion.

TABLE I. *Central Illinois artificial lakes (Figs. 1, 2, 3, 4, 5)*

Name of lake	Location	Stream	Size; acres or miles	Bot- tom	Depth, m.	Built	pH	O ₂
Patterson Springs ¹	Camargo	.	38 a.	Mud	0-15	1927	7.6	5.23
Bloomington	Bloomington	Money Cr.	$\frac{1}{4} \times 3$ m.	Mud	0-30	1930		4.36
Vermillion	Danville	Vermillion River	$\frac{1}{2} \times 3$ m.	Mud	0-30			
Above old dam						1913	7.7	5.1
Below old dam						1926	7.8	4.78
West L.	Paris	Sugar Cr.	$1\frac{1}{4} \times 8$ m.	Mud	0-14	1895		
East L.	Paris	Sugar Cr.	$\frac{3}{4} \times 4$ m.	Mud	0-14	1916		
Decatur	Decatur	Sangamon	$\frac{1}{2} \times 13$ m.	Mud	0-25	1927	7.8	
Carbondale	Carbondale	Piles Fork Cr.	80 a.	Mud	0-20	1926		

¹ Patterson Springs is for recreation and fishing and not for a supply of water.

The land inundated in all cases was typical flood plain land, either cultivated or woodland. In many cases the tree stumps were not removed before flooding occurred.

Stream Habitats

The region studied is in Central Illinois in the Counties of Champaign, Piatt, McLean, Edgar, Douglas, Vermillion and Coles. The greater portion of this area lies in the Grand Prairie Region (Vestal, '30). Much of this region was originally swampy, but since the establishment of artificial drainage, the excess surface water is quickly removed. In general, the area is a glaciated gently rolling plain, relatively free from rock fragments and broken by narrow belts of more rolling to slightly hilly country bordering the major stream valleys. The streams studied (fig. 6) were the Sangamon River and its tributaries, Fox Run, Goose Creek, and Camp Creek.

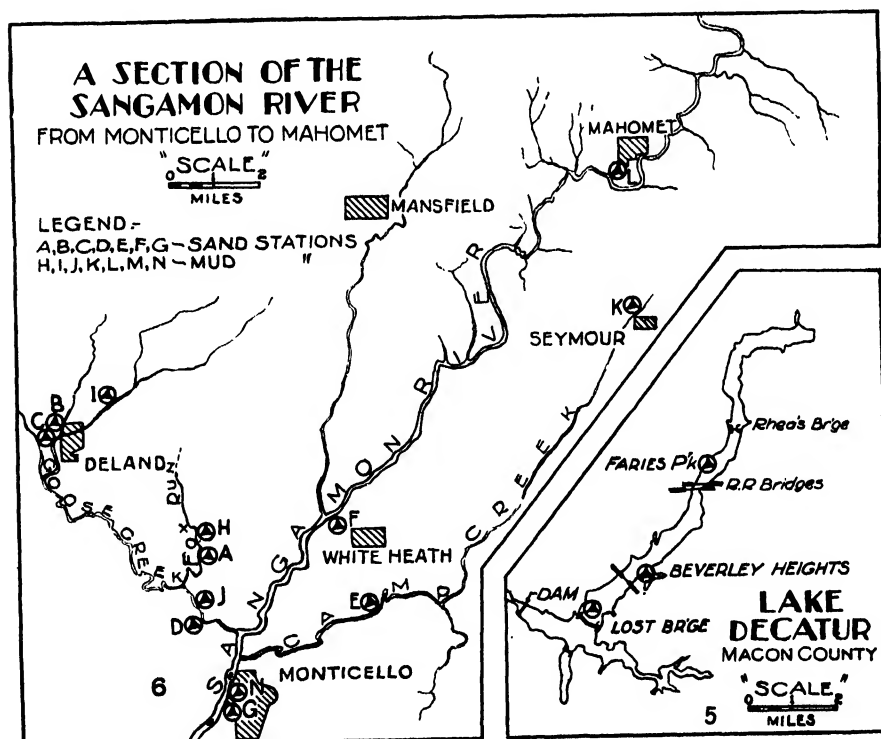


FIG. 5. Lake Decatur, Decatur, Illinois.

FIG. 6. A section of the Sangamon River showing the location of the stations studied.

The Sangamon River is a comparatively small turbid stream of a type which is common in Central Illinois. The bottom is composed principally of shifting sand and gravel although there are short pools or sluggish stretches

where silt is deposited. The sandy bottom at any given place is constantly being changed. Notwithstanding this fact, it is stable enough in some locations to maintain populations which have remained essentially the same for four years. The Sangamon River, a tributary of the Illinois River, has a drainage area of approximately 5390 square miles and is about 237 miles long. It rises in McLean County and flows through Champaign, Piatt, Macon, Sangamon, Menard, Case and Mason Counties. The distance from the source to Decatur is about 103 miles. The current is never very great at its normal level as the river falls only 120 feet per mile for the remainder of its course. There are some areas where the gradient is very slight. Along its shores and floodplain may be found the typical floodplain trees and shrubs, which stabilize the banks and provide shade.

Camp Creek (fig. 6) rises in Champaign County and flows' in a south-westerly direction. Near its headwaters (Seymour), the bottom is composed of silt to a depth of several inches, but at its mouth (Monticello), the bottom is almost entirely of pure sand and gravel.

Goose Creek, an intermittent stream rising in cultivated fields, originally prairie, enters the Sangamon River about one-half mile above Camp Creek. The greater part of the bottom is composed of sand and gravel. However as in the case of the Sangamon River there are spots where silt is deposited. Fox Run is a tributary of Goose Creek entering the Creek about four miles north of Monticello.

The water in Goose Creek and Camp Creek is clear, varying in depth from about six inches (15 cm., Fox Run), to one and one-half feet. The average depth of the Sangamon is about two feet (60 cm.). The rate of flow of the Sangamon at Mahomet and Monticello is about one-half mile per hour during the summer (Eddy, '32). Further down the river at Chandlerville and Petersburg, it averaged a little more than one mile per hour. There is no perceptible current in the main part of Lake Decatur. The average rainfall as recorded for Decatur for a period of thirty-four years (prior to 1929) is 38.07 inches (Smith, *et al.*, '29). About half of this comes in the spring and growing season. The wettest year on record had a total rainfall of 60.58 inches, and 1926 had a total rainfall of 56.68 inches. The driest year on record (1914) had a total rainfall of 25.10 inches. As an illustration of extremes it is noted that 16.56 inches of rain fell in September 1926 and only 0.07 inches in November 1904. In 1929 the level of the Sangamon River at Decatur varied three and one-half feet (105 cm.) between June and September.

QUASI-EXPERIMENTAL COMMUNITIES OF ARTIFICIAL POOLS

Streams in this section of the country are characterized by alternating areas of pools and rapids (Shelford, '13). These are areas of the stream in which the current is, very slow in portions and where the current is more rapid

in other portions. The formation of pools by outcropping of rock in the stream bed is not an uncommon occurrence. Thus, when artificial pools are formed by the water supply dams, conditions are created which are characteristic of undisturbed stream bottoms. In some cases this duplication generally results in the formation of a somewhat larger pool than would ordinarily be found in a stream of the size of the one dammed. The bottoms of these newly formed pools are at first without animal life, *i.e.* bare areas upon which communities develop. They must in the main be populated from the pools of the streams that have been dammed.

A stream community includes three layer communities usually treated separately, namely: *plankton*, *fishes*, and *bottom fauna*. This paper is concerned primarily with the bottom communities which are subordinate or layer communities. The plankton was studied by Eddy ('34) and fishes were discussed by Thompson and Hunt ('30).

Chironomus plumosus Community

Lake Bloomington, studied in November 1930 (table II), some five months after its completion (6.xi.30), had a fairly large population of *Chironomus plumosus* L. (bloodworm), close to the shore in water not more than

TABLE II. *Lake Bloomington, Bloomington, Illinois. Filled in November, 1929*

Species	Number of individuals per square meter and date		
	6.xi.30	7.vi.31	29.x.31
<i>Chironomus plumosus</i> L.....	29	84	
<i>Corethra</i> sp.....		108	88
<i>Procladius</i> sp. no. 2.....			4
<i>Ceratopogonidae</i>			4

five feet deep. Bottom samples during the following summer yielded only *Corethra* larvae in the deeper portions of the lake (25 feet; 8.1 meters deep) although *C. plumosus* was still more abundant near the shore than in the previous fall; an amphipod, and *Ranatra fusca* were associated with it. These species are all common stream animals, and probably derived from the stream concerned.

The following fishes are all in streams of the size that were dammed: the gizzard shad, *Dorosoma cepedianum* (Le Sueur); blunt-nosed minnow, *Pimephales notatus* (Rafinesque); black bullhead, *Ameiurus melas* (Rafinesque); common shiner, *Notropis cornutus* (Mitchill); little pickerel, *Esox vermiculatus* Le Sueur; top minnow, *Fundulus notatus* (Rafinesque); the blunt-nosed

river carp, *Carpiodes difformis* Cope; redhorse, *Moxostoma breviceps* (Cope). The gizzard shad and the blunt-nosed minnow are among the first to expand in population. The gizzard shad is regularly introduced into such waters to supply food for game fishes which are also planted. They feed on detritus, and animal life of the bottom, and increase with the beginning of its presence. *Corethra* and *Chironomus* larvae at times constitute a very large portion of the food of the gizzard shad.

Chironomus plumosus has a tendency to occupy the shallower water at first. As the population becomes greater this species tends to migrate out toward the middle of a body of water or toward the deeper portions. This was observed to be true at Lake Bloomington (fig. 4; table II) in the fall of 1930, Lake Decatur (fig. 5), in the summer of 1931, and Lake Vermillion (table IV; fig. 3) in September of 1931. The deeper portions of Lake Decatur and Lake Vermillion have only *Corethra* sp. and *C. plumosus*. The greatest depth of these two lakes is approximately 25 feet (8.1 meters). This depth is somewhat greater than one will ordinarily find in a central Illinois stream and probably should not be considered as a stage in pool succession. Samples from these depths were always ill smelling and consisted of decaying sticks, grasses and other organic matter. As the area becomes older the animal population tends to become more uniformly distributed, so that in the oldest area studied the animal population near the shore did not differ from that found in the deeper portions of the pool (table IX, Twin Lakes).

TABLE III. *Patterson Springs Pond, Camargo, Illinois. Filled September, 1927*

Species	Number of individuals per square meter and date, 1931		
	22.vi.	9.ix.	27.x.
<i>Chironomus plumosus</i> L.....	564	25	204
Ceratopogonidae.....		6	2
Leeches (small).....	8..		
<i>Limnodrilus</i> sp.....	12		
<i>Perithenius tenera</i> Say.....	4		

Chironomus plumosus characterizes the early stages of the development (tables II, XI, and XII). It soon reaches a maximum abundance in both stream and artificial pool habitats (tables III, XI, and XII), and rapidly declines in importance although it still continues to be a member of the most stable community (fig. 7, 11; table IX). Both stream and pool habitats exhibit a general lack of food material.

Chironomus plumosus belongs to a group of animals which require very little food (Leathers, '23), and has a comparatively short life history, so it

seems to be ideally adapted for life in a pioneer stage. *Corethra* which is pelagic at night often comes in early. It feeds on Infusoria, small Crustacea, and small larvae, including those of mosquitoes (Comstock, '25). It serves as food for fishes. When a dam is filled, the deposition of detritus and silt begins at once but the small amount of plankton in the water first filling the

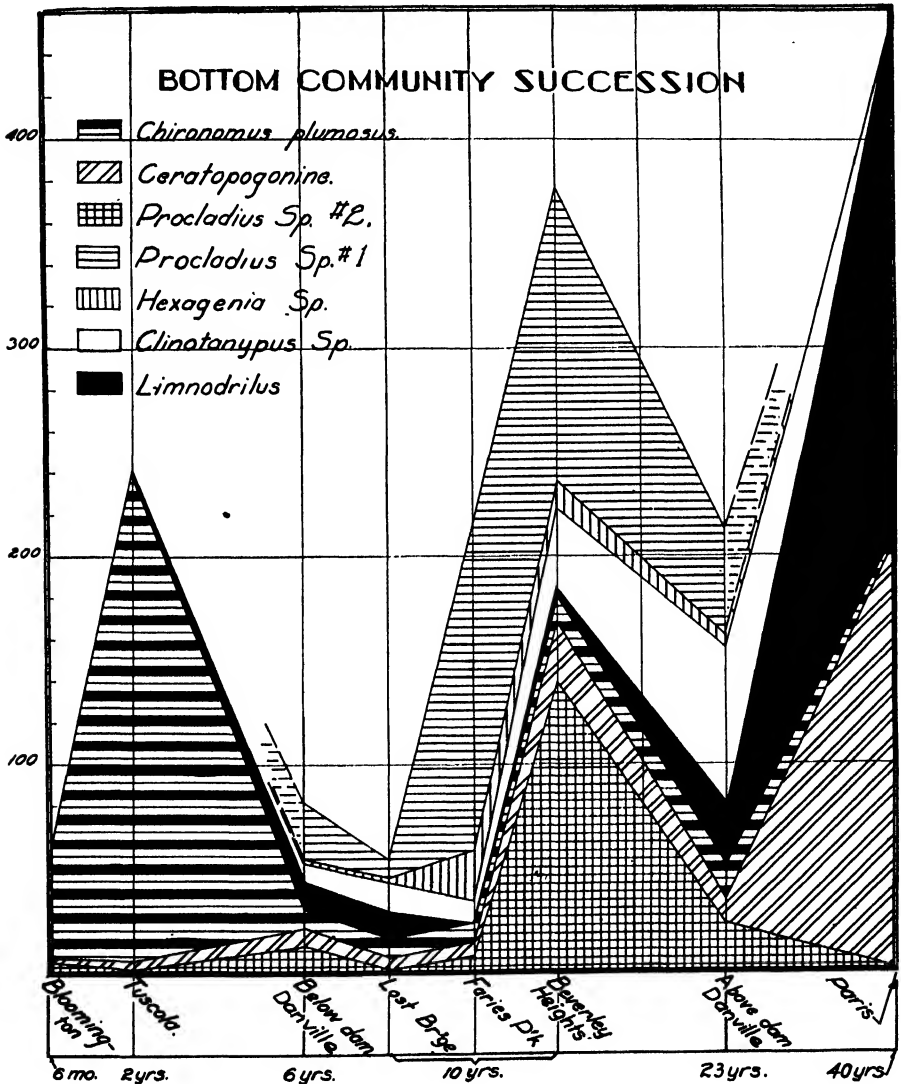


FIG. 7. A graphic representation of the succession of the bottom communities of the quasi-experimental areas. The three definite peaks in the graph represent the maximal abundance of different species of animals upon different ages of lake bed. Each peak represents a facies in the development of the community.

pool requires some weeks for increase and the layer of bottom detritus which is probably essential to various bottom forms accumulates at an unknown rate. The plankton of Lake Decatur was great in quantity the year following the filling of the dam. *Eudorina* was the most abundant type in 1923 (Eddy, '34), but was succeeded by other prevalents in succeeding years with the addition of various species new to the community. While it is not known whether changes in the plankton community and the consequent changes in the nature of the detritus are important to the bottom inhabitants, the age of the bottom is probably significant.

Since the plankton or plankton remains form a large portion of the food of bottom dwellers, a population of these animals cannot develop until plankton or surface algae are present. Standing water develops a plankton population much more rapidly than running water. As a result there is a better food supply developing in the artificial and natural pools of the stream. The plankton when it dies finds its way to the bottom, where it becomes mixed with the remains of filamentous algae, other plants, and the decaying bodies of larger animals that have been unable to reach maturity on such areas or which have died from various reasons. This material forms a thin layer of organic material over the bottom of the stream, which is much thicker in the months of July, August, and September because of the continual building up of the layer after the spring rains have ceased. Data collected shows that the thickness of this layer decreases in October. The probable cause of this decrease in thickness is the great amount of silt brought in by the run-off of the fall rains which tend to cover up the bottom deposits. . An abundance of bacteria may be assumed as soon as the organic matter begins to accumulate and is further indicated by the presence of bacteria-feeding ceratopogonid midge larvae. There is also a fairly abundant population of microscopic organisms (blue-green algae, rotifers, Protozoa, etc.).

Copepods secured by means of the glass tube method of sampling would swim to the top of the tube (about fourteen inches) and then turn and make a head-long dive into this flocculent mass. There they created quite a commotion as they proceeded to make their way below the surface of this layer. They, together with the annelid worms belonging to the genus *Limnodrilus*, would tend to keep the layer well aerated. The composition of this detritus layer needs further study and affords a subject for separate investigation. A detailed study of this layer will be necessary before an adequate understanding of the development of the bottom communities can be had.

That the physical nature of the bottom is a factor aside from the organic detritus is indicated in the two portions of the lake formed by the new dam at Danville (fig. 3). The upper half of the present lake represents a bottom laid down in an old dam between 1913 and 1932. The bottom was dry in all portions of the lake except in the old stream course from 1924 to 1926. The more rapid development of the communities on the old bottom is indicated by a comparison of the data in tables IV and VIII. The old bottom gained

from 1 to 3 years. The organic detritus, probably disappeared during the time the bottom was dry, and the results were attributable to the accumulation of terrigenous materials of the smallest possible size.

The Ceratopogonidae and *Procladius* sp. no. 2 (midge larva) invade in small numbers soon after *Chironomus plumosus* has developed a good population. *Procladius* appeared in Lake Bloomington (table II) when it was one year of age. Nearly three years elapsed before Patterson Springs Lake (table III) was studied and at that time, *Limnodrilus* sp. was found in relatively small numbers.

TABLE IV. *Vermillion Lake, Danville, Ill. Below old Dam. Filled in 1926.*
A = Abundant. P = Present

Species	Number of individuals per square meter and date										
	1928	1929		1930			1931				1932
	16.x.	5.ix.	5.x.	3.v.	25.x.	26.vi.	1.viii.	4.ix.	15.x.	24.x.	11.i.
<i>Corethra</i>	A	16					117	124	176	13	212
<i>Chironomus plumosus</i> L.		8	1	5	58	4	6				
<i>Clinotanypus</i> sp.		8	1				8			26	13
<i>Procladius</i> sp. no. 2				5	39					17	2
<i>Limnodrilus</i> sp.					P		13	8	14		P
<i>Tubifex</i> sp. (Annelid)						4					
<i>Hexagenia</i> sp.						13					
<i>Procladius</i> sp. no. 1							4	24	P		26
<i>C. plumosus ferrugineovittatus</i> Sett.							1				
<i>Gordius</i> sp.								1			
Ceratopogonidae									14	4	17
Amphipods											17

The changes in the population of the species of fishes which become abundant later are much more difficult to follow, and the changes which take place are not a part of this investigation. The large-mouth black bass, *Micropterus salmoides* (Lacépède); small-mouth black bass, *Micropterus dolomieu* Lacépède; rock bass, *Ambloplites rupestris* (Rafinesque); calico bass, *Pomoxis sparoides* (Lacépède); white crappie, *P. annularis* Rafinesque; yellow perch, *Perca flavescens* (Mitchill); yellow bass, *Morone interrupta* Gill; and the channel cat, *Ictalurus punctatus* (Rafinesque) are the favorite species for

planting, having been repeatedly stocked in all of the ponds. The young hickory shad is important as food for the piscivorous species and the minnows also play an important rôle throughout development and in the later stable stages. An inspection of tables II to VI and of fig. 7 shows that between five and ten years, *Chironomus plumosus* decreases to a small population while several others, especially two species of *Procladius* increase to points of predominance and *Hexagenia* (mayfly nymph) and *Musculium* also appear. Because of their size the two later forms are of considerable significance.

Hexagenia-Musculium Bottom Community

With the ageing of the habitat, the *Chironomus plumosus* community is invaded by *Hexagenia*, *Musculium*, and freshwater mussels (Unionidae). *Hexagenia* awaits the covering of the original bottom of rough soil or meadow grass with soft flocculent silt and detritus into which it can burrow readily. Similar conditions are necessary for bivalves, especially in the young stages. It must be inferred, however, that pelagic life plays a larger rôle than the bottom forms. It is further essential as a source of food. The number of small active rotifers, etc., increase with the increase in the flocculent detritus layer and such animals provide food for the predatory *Clinotanypus* (midge larvae). With the progress of silting the invaders gain ascendancy in numbers. This bottom layer community takes the place of the *C. plumosus* community in about ten years when *Hexagenia*, *Musculium* and the Unionidae shown in tables VII and VIII have gained ascendancy.

Many of the fishes of the *Chironomus plumosus* Community are also found in this community. The white perch, *Aplodinotus grunniens* Rafinesque; blunt-nosed river carp, *Carpiodes difformis* Cope; common red horse, *Moxostoma aureolum* (Lé Sueur); short-headed red horse, *Moxostoma breviceps* (Cope); red-mouth buffalo, *Ictiobus cyprinella* (Cuvier & Valenciennes); European carp, *Cyprinus carpio* L.; and the common sucker, *Catostomus commersonii* (Lacépède), are newcomers to the community. It is noteworthy that the greater portion of these species utilize the bottom inhabitants as the main source of their food supply. These fishes are not so abundant in Lake Decatur and Lake Vermillion as they are in older pools.

Local Variations in the Community and Habitat

Currents and Waves

Hexagenia sp. (*bilineata*) and *Limnodrilus* sp. are usually totally absent from communities with considerable current. These reach their maximum abundance where small bays, points, etc. offer conditions in which there is little disturbance of the bottom. Such a condition is well illustrated at Faries Park and Beverly Heights (fig. 5), at Lake Decatur (table V, 1930, and June 1931 for abundance of *Hexagenia* and table VII for abundance of *Hexagenia* and *Limnodrilus*). Faries Park is located near the upper end of the

lake. The water is comparatively shallow, and a current can be detected. Near the west shore and extending out for some distance bottom material is very fine and readily goes through the sieve without leaving any debris. Farther out where the bottom is swept by the current, the samples, although appearing to be essentially the same materials as those found near the shore, are almost impossible to screen so that the animals may be found. This black clay-like material, which resembles small pebbles, has been brought in by the

TABLE V. *Lake Decatur at Faries Park, Decatur, Ill., filled June 27, 1922.*
A = Abundant. P = Present

Species	Number of individuals per square meter and date					
	1926, 1927, 1930	1931				
		29.vi.	31.vii.	4.ix.	6.x.	2.xi.
<i>Anodonta grandis</i> Say	A					*
<i>Lasmigona complanata</i> (Barnes)	P					*
<i>Musculium transversum</i> (Say)	12					
<i>Hexagenia bilineata</i> Say Mayfly nymph	54	5				
<i>Chironomus plumosus</i> L.	12	5		4	6	
<i>Procladius</i> sp. no. 1	24	117	299	32		2
<i>Procladius</i> sp. no. 2		8		4	2	
<i>Clinotanypus</i> sp.		13	17	8	2	
Ceratopogonidae		5	4	8		
<i>Corethra</i>			27			
<i>C. plumosus ferrugineovittatus</i> Zett.			4			
<i>Proptera alata megaptera</i> (Raf.)						*

* = Estimates of 1 per square meter each for *Anodonta grandis* (mussel), *Lasmigona complanata* (mussel) and *Proptera alata megaptera* in the near shore community.

river and dropped as soon as the current is slowed. The difference in bottom life is striking. Near the shore the prevalent animals are *Hexagenia* sp. (15–20 per square meter), and *Musculium transversum* (Say) (finger nail snail). The latter animal is fairly abundant although not so numerous as *Hexagenia* sp. As soon as one passes into the area in which this clay-like material is found, *Hexagenia* sp. disappears and *Procladius* sp. no. 1 becomes abundant. In fact *Procladius* sp. no. 1 and *Corethra* sp. are generally the only animals present in such a habitat. The area occupied by *Hexagenia* sp. is

undoubtedly older from a community point of view than the habitat occupied by *Procladius* sp. no. 1. The two areas although within fifty feet of each other have different animal populations. Current is undoubtedly a determining factor in this case. Wind can also exert quite a force in disturbing the bottom. Large waves are not uncommon on Lake Decatur.

Beverly Heights station (fig. 5) is a small bay which is not affected by the current. There is no disturbance of the bottom except from wind. This is not great owing to the protection afforded by high surrounding banks. As the bay is sheltered, only west winds have an unobstructed sweep across it.

TABLE VI. *Lost Bridge, Lake Decatur, Decatur, Ill. Dam completed in June, 1922.*
P = Present

Species	Number of individuals per square meter and date						
	1927	1930	1931				
	8.x.	18.x.	29.vi.	3.vii.	3.ix.	6.x.	2.xi.
<i>Corethra</i> sp.	44	P	3	67	44	132	10
<i>Musculium transversum</i> (Say)	4	P	15		2	2	
<i>Hexagenia bilineata</i> Say	P		3		2		
<i>Chironomidae</i>	22	P (3 sp.)					
<i>C. plumosus ferrugineovittatus</i> Zett		13	43	15	2	17	
<i>Clinotanytus</i> sp.			13			40	17
<i>Chironomus plumosus</i> L.			5	8	22	2	6
<i>Limnodrilus</i> sp.				6		21	
<i>Procladius</i> sp. no. 1					10	7	
<i>Ceratopogonidae</i>					4	7	5
<i>Sphaerium occidentale</i> Prime							1

High bluffs on the north and south protect the area. The writer, in making observations from this area, found that when a wind was blowing from the southwest, and when the waves in the surrounding water were high, there was a zone of quiet water marked by the small bay. When the bottom of the bay was examined for animals (table VII), it was found that the distribution of *Hexagenia* sp. coincided very closely with the area of still water. Other important members of the community were *Sialis infumata* Newman, *Musculium transversum* (Say), and *Limnodrilus* sp.

Similar bays studied in Lake Vermillion have yielded like results. An old settling basin at Danville, the bottom of which resembled that of the bays,

had a population of over 20 *Hexagenia* nymphs per square meter in 1930. These areas are fairly stable and are more nearly comparable to conditions existing in a base-leveled stream and are older ecologically than the areas affected by the current and wind. There are areas in streams which develop more rapidly than other areas; consequently actual age in years of a stream bottom would not necessarily be an index as to the type of community existing there. Wind and current must then be considered as factors in keeping an

TABLE VII. *Beverly Heights, Lake Decatur, Decatur, Ill. Dam completed in June, 1922. P = Present*

Species	Number of individuals per square meter and date							
	1926	1927	1930	1931				
		8.x.	18.x.	29.vi.	3.vii.	4.ix.	6.x.	3.xi.
<i>Limnodrilus</i> sp.	1					2	6	4
<i>Anodonta grandis</i>		P						
<i>Chironomidae</i>			7					
<i>Hexagenia bilineata</i>				39		6	6	9
<i>Chironomus plumosus</i>				13	60	24	24	17
<i>Clinotanytus</i> sp.				130	17	6	34	26
<i>Procladius</i> sp. no. 1				390	47	108	6	
<i>Corethra</i> sp.				60	30	18	60	9
<i>C. plumosus ferrugineovittatus</i> Zett				4	9	4		
<i>Procladius</i> sp. no. 2					9	6		
<i>Musculium transversum</i>				P	9	2	2	4
Ceratopogonidae						14	58	13

area young ecologically. Much less variation is to be expected in base level spots.

Excessive Silt

Silting has been going on very rapidly in Lake Decatur. Thus a creek at Beverly Heights, 20 feet (6.5 meters) wide and six feet (2 meters) deep, which was submerged in 1922 has now become filled with silt so that it is the same level as the surrounding bottom. This rapid silting has undoubtedly had an effect upon the animals previously found there. It has been previously

reported (Baker, '28; Shelford, '29; Shelford and Eddy, '29) that fairly large numbers of the large floater *Anodonta grandis* Say and the snail *Campeleoma* sp. occurred there about 1926 and 1927. The writer, although having made numerous hauls with the Peterson bottom sampler and with the triangular dredge, has failed to find a single living specimen of *Anodonta grandis*, although numerous dead shells have been brought up, and there are great numbers of these shells to be seen half-buried in the shore. It seems that *Anodonta grandis* as well as other Unionidae have entirely disappeared from the

TABLE VIII. Vermillion Lake, Danville, Ill. Above old Dam. Filled 1906.

Species	Number of individuals per square meter and date								
	1929	1930		1931					
	5.x.	3.v.	25.x.	26.vi.	1.viii.	5.ix.	15.x.	24.x.	31.xi.
<i>Corethra</i> sp.	160	32	175	78	26	272	720	158	602
<i>Chironomus plumosus</i>	32		26	18	4		2		8
<i>Procladius</i> sp. no. 1	112	38		5	4	30	22		145
<i>Procladius</i> sp. no. 2	48	17	26		13	8	16		17
<i>Clinotanypus</i> sp.		90	26	119	8	16			15
<i>Limnodrilus</i> sp.		42	117	22	14	9	2		12
Ceratopogonidae		16	26						2
<i>Hexagenia bilineata</i>				6			2		
<i>Tubifex</i> sp.				58	20	31	6		5
Amphipods									2
<i>Carunculina parva</i>									2 in qual.

lower portion of the lake owing to the excessive amount of silting. Juvenile mussel development upon a mud area is hazardous due to the fact that the young clams may sink into the mud and be smothered; sand is much better for the early stages. These mussels after they reach some size may migrate to mud areas with safety. This perhaps accounts for the great number of mussels at Faries Park (table V; fig. 5) where there is an area of sand near the mud. *Anodonta grandis*, *Proptera alata megalptera*, and *Lasimigona complanata* are well represented at this place. The last two species reach extremely large sizes here.

This state of community development is comparable to the base-leveled stream of medium size. Such variation in bottom and current is of regular occurrence in the pools of large base-leveled streams but exaggerated in differentiations due to the relatively great importance of wave action against irregular topography with bays and jutting points as compared with a longitudinal flow in a river channel. These variations are of importance to the bottom communities. The result is the various faciations of the community. The community found in these middle age artificial pools is climax.

The attention of the reader is called to figures 8-11, which represent a sequence of stages in succession on similar bottoms of different age (cf. 8, 9, and 11) and rate of flow (cf. 9 and 10) which have just been discussed. The animals are approximately one-half natural size, and thirteen times as abundant as they would appear on a similar area on the lake bottom. The lake at Paris agrees in general with Lake Vermillion data, except in a great increase in the number of annelid worms and in the disappearance of *Hexagenia* nymphs, and *Procladius* sp. no. 1 larvae. Figure 10 of the near shore community at Faries Park is the same community which is found above the old dam in Lake Vermillion. Protection from winds and waves, and the deposition of great amounts of silt have resulted in the more rapid development of this community than of nearby areas in the open water. The number of animals represented is as follows: (1) On a 0.1 square meter (fig. 8) of bottom of a one year old lake (Lake Bloomington) *Corethra* sp., 10; *Chironomus plumosus*, 8. (2) On 0.1 square meter (fig. 9) of bottom area of a ten year old lake (Faries Park in current, Lake Decatur) *Procladius* sp. no. 1, 11; *Clinotanytus* sp., 2; *Chironomus plumosus*, 1; *Ceratopogonids*, 1; *Corethra* sp., 1. (3) The representation of a square meter area of bottom (fig. 10) in the near shore community at Faries Park in Lake Decatur, enables some animals to be shown which are not abundant enough to appear in a representation of a 0.1 square meter of bottom area. The animals are drawn to scale and are shown one hundred and thirty times more abundant than they would appear on a similar area on the lake bottom: *Chironomus plumosus*, 6; *Hexagenia* sp., 6; *Corethra* sp., 20; *Procladius* sp. no. 1, 25; *Clinotanytus* sp., 10; *Musculium transversum*, 3; *Ceratopogonids*, 3; *Proptera alata megaptera*, 1; *Anodonta grandis*, 1. (4) On 0.1 square meter (fig. 11) of bottom area on a twenty-five year old lake bottom (above old dam, Danville, Illinois): *Corethra* sp., 20; *Limnodrilus* sp., 2; *Chironomus plumosus* L., sp., 1; *Procladius* sp. no. 1, 2; *Hexagenia* sp., 1; *Ceratopogonidae*, 2; *Clinotanytus* sp., 2.

Secondary *Ceratopogonidae*-*Limnodrilus* Community

This community is well illustrated (table IX) by the pool at Paris (completed in 1895). The water there is always very quiet because the lake is not large enough for the waves to affect materially the extremely soft, organically rich bottom, which has been built up by silt and detritus. The bottom sampler

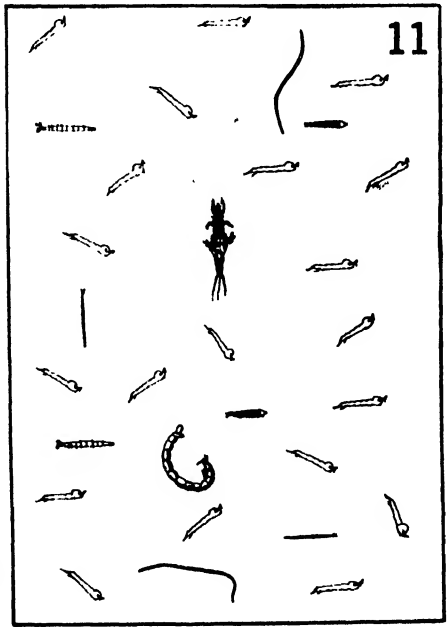
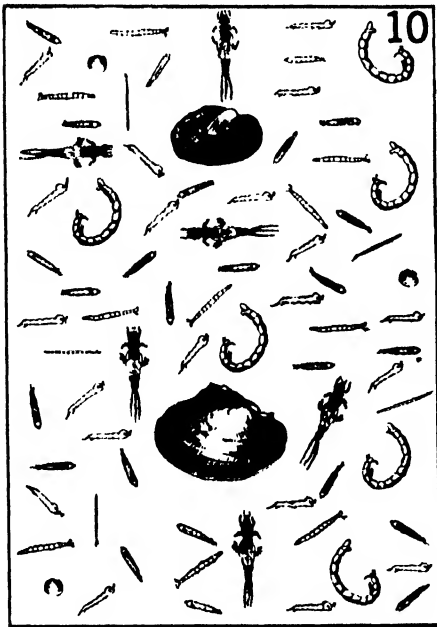
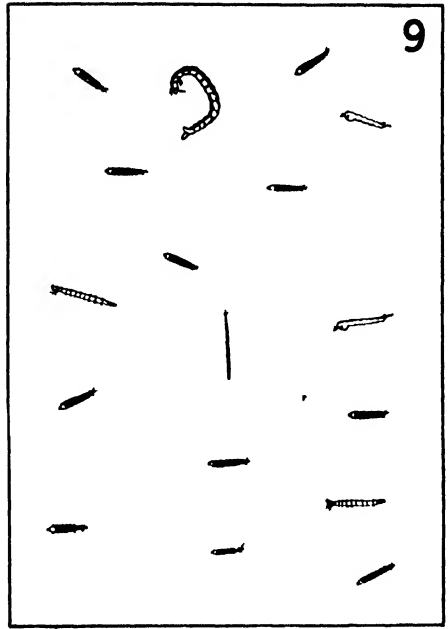
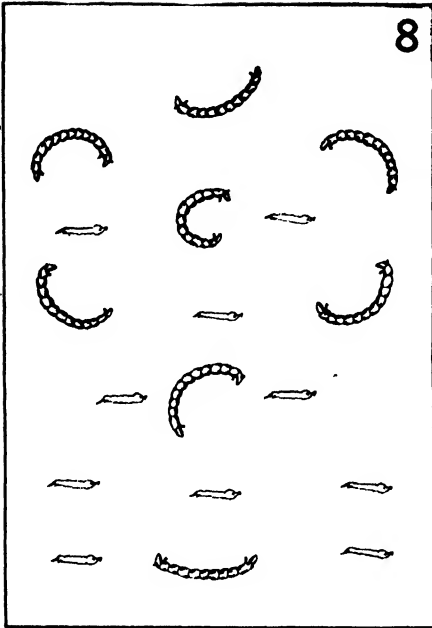


FIG. 8. One year old bottom (Lake Bloomington), 0.1 square meter.

FIG. 9. Ten year old bottom (Faries Park in current), 0.1 square meter.

FIG. 10. Ten year old bottom (Faries Park, Lake Decatur), 1.0 square meter.

FIG. 11. Twenty-five year old bottom (above old dam, Danville), 0.1 square meter.

always came up filled to the top with mud oozing through small holes in the upper half. This would indicate that the mud is soft and deep. The *Hexagenia* nymphs and *Procladius* sp. no. 1 had disappeared (fig. 7) probably on account of increased organic matter, and in their place two other prevalents, *Limnodrilus* sp. and a ceratopogonid, characterized the community.

TABLE IX. *West Lake, Paris, Illinois. Dam completed, 1895. P = Present*

Species	Number of individuals per square meter and date, 1931				
	25.vi.	2.viii.	11.ix.	8.x.	4.xi.
<i>Limnodrilus</i> sp.	572	288	184	112	52
<i>Corethra</i> sp.	4	544	208	160	26
Ceratopogonidae	52	28	192	176	104
<i>Chironomus plumosus</i>	4	4			
<i>Clinotanypus</i> sp.				P	
<i>Procladius</i> sp. no. 2				P	

TABLE X. *East Lake, Paris, Illinois. Dam completed, 1916*

Species	Number of individuals per square meter and date, 1931	
	Lower end 11.ix.	Upper end 11.ix.
<i>Chironomus plumosus</i>	32	24
<i>Corethra</i> sp.....	36	8
Ceratopogonidae.....	284	364
<i>Limnodrilus</i> sp.....	4	
<i>Clinotanypus</i> sp.....	4	
<i>Procladius</i> sp. no. 2.....		8

These prevalents are fairly evenly distributed over the entire bottom of the pool. The ceratopogonid was most abundant (1932) in the parts of the Paris pool which had been dry and vegetation covered in 1931, which suggests its high requirements for organic matter. This vegetation was undergoing decomposition in 1932.

LONGITUDINAL SERIES OF STREAM HABITATS AND THEIR COMMUNITIES

To secure a comprehensive view of the stream system studied one must lay aside all theory of stream development and view the Sangamon River and its tributaries in order to classify the habitats and communities.

These are of four types: (1) Rapids with bottom of coarse gravel—rapid water communities—rare in the Sangamon and not considered here. (2) Semi-pools with *Pleurocera*. (3) Sand bottom pools. (4) Mud or silt bottom pools.

Adams ('01) pointed out that dispersal of aquatic animals is determined by the shifting backward of the headwaters and other conditions in streams as erosion occurs. Thus the animal life of the river pushes upward in the tributaries as erosion goes on, and the animals of the headwaters push farther upstream. This must be considered as occurring in a very general way, reducing the more rapid water and increasing the sluggish water in the lower part of the stream.

Considering stream development as taking place over one given area, by securing data from the head waters of a stream and from the main stream itself, together with data from intermediate points on these streams, theoretically one may predict the series of communities which will follow one another over a given point. The headwaters are the youngest portion of the stream. These headwater streams are gradually approaching the condition of a wider portion of the stream. In fact these headwaters, in some cases, may be considered to represent the size of the main stream thousands of years ago. From the standpoint of this paper, however, the study of the normal stream was to verify and interpret what may be found there in the light of the study made of artificial pools.

Mud Bottom Pools

A bottom layer community of the mud bottom pool (table XI) may be found even in intermittent streams during rainy periods. A series of pools of various sizes is to be found in medium-sized creeks from their source to the Mississippi River.

Chironomus-Chironomus Mud Bottom Community; Intermittent Creeks

This community occurs in intermittent streams such as Fox Run and Goose Creek (fig. 6), in the area of study. The flow of water varies greatly and is influenced to a great extent by each rain. The width of the streams may vary from one to several feet. *Chironomus plumosus* and *C. sp. (fulviventris?)* exceed all other members of the community in numbers (table XI). Tabanidae (larvae), *Orthocladus sp. (larvae)*, *Palysonomyia sp. (larvae)*, *Cambarus propinquus* (Girard), *Eucrangonyx gracilis* Smith, and *Blasturus cupidus* Say, etc., are members of the community. Even in the earliest stages studied scattered individuals of *Hexagenia sp.* and *Limnodrilus sp.* may be found associated with the prevalents *Chironomus plumosus* and *C. sp. (fulviventris?)*. The fishes of this community are the horned dace, *Semotilus atromaculatus* (Mitchill); and the blunt-nosed minnow *Pimephales notatus* (Rafinesque); and the young of the common sucker which goes into the small tributaries to spawn. This layer community is clearly a *developmental* stage comparable to those in the new pools formed by dams but because of drying and flooding, it is repeatedly destroyed (see page 268).

The maintenance of this community is similar to that of the communities in artificial pools. The amount of plankton and detritus is less but the organic matter from the land, filamentous algae, other bottom organisms, and midsummer rooted plants is increased by the severe fluctuating conditions.

The intermittent stream communities can rarely go beyond the *Chironomus plumosus* stage. Wherever the water is permanent, however, this bottom layer community progresses through the addition of *Hexagenia* sp. and *Limnodrilus* sp. which characterize the climax in all the stream pools.

TABLE XI. *The distribution of the animals over the mud bottom as found at the various stations along the streams*

h (Fox Run), i (Deland), and j (Monticello) are stations in Goose Creek. k (Seymour) is located in Camp Creek and l (Mahomet), m (White Heath), and n (Monticello) are in the Sangamon River. Station h is the youngest of the physiographic mud succession and n is the oldest stage of the same succession.

	h	i	j	k	l	m	n
* <i>Chironomus plumosus</i>	28	10	40	6	7	11	2
<i>C. near fulviventr</i> is	40	134	50	16	1		
* <i>Hexagenia bilineata</i>	4	3	3		20	14	3
* <i>Limnodrilus</i> sp.	2		90		17	1	
Tabanidae (larvae)	1	1	2		2	2	
<i>Orthocladius</i> sp.	8			6			
<i>Physa gyrina</i>	2			2			
* <i>Palpomyia</i>		4			10		
* <i>Pisidium</i> sp.		2		10			
<i>Cambarus propinquus</i>			3				
* <i>Sialis infumata</i>			1		1		
<i>Mancasellus macrouris</i>				40			
<i>Eucrangonyx gracilis</i>				4			
<i>Blasturus cupidus</i>				0.4			
<i>Heptagenia interpunctata</i>				4			
* <i>Chironomus</i> sp.				2			
*Leeches				1			
<i>Tritogonia verrucosa</i>					0.3		
<i>Tanypus</i> sp. no. 1					0.3		
<i>Tanypus</i> sp. no. 2					0.3		
<i>Proptera laevis</i> sima					0.3		
* <i>Musculium transversum</i>							0.2
<i>Lampsilis ventricosa</i>							0.1
<i>Gomphus spiniceps</i>							0.1

* These species are also found on the quasi-experimental areas.

Hexagenia-Musculium-Limnodrilus Mud Bottom Community of Small Rivers

This community occurs in permanent water varying in depth from four inches to three or more feet, in favorable seasons. Because of the rapid replacement, motility, and short life span this layer community may invade non-permanent waters during rainy periods covering two or more years in which stream levels remain high.

In the still water pools of the Sangamon River and the lower part of Camp Creek, near Monticello, the *Chironomus plumosus* bottom layer com-

munity is less often encountered than in the smaller streams. Its place is taken by a community in which *Hexagenia* sp. and *Limnodrilus* sp. are prevalents. *Limnodrilus* comes into the later stages of succession and into communities where considerable organic matter occurs. The prevalents of the community are *Hexagenia* sp., *Chironomus plumosus*, and *Limnodrilus* sp., and *Musculium transversum* (Say). Other animals of lesser importance are *Pisidium* sp., *Tritogonia verrucosa* (Raf.), *Tanytus* sp. no. 1, *T.* sp. no. 2, *Proptera alata megaptera* (Raf.) *Tabanidae* (larvae), *Lampsilis ventricosa* (Barnes), *Anodonta grandis* Say, and *Gomphus spiniceps* Walsh.

The dominants are fishes including the white perch, *Aplodinotus grunniens* Rafinesque; Gizzard shad, *Dorosoma cepedianum* (Le Sueur); blunt-nosed river carp, *Carpiodes difformis* Cope; common red horse, *Moxostoma aureolum* (Le Sueur); short-headed red horse, *M. breviceps* (Cope); red-mouth buffalo, *Ictiobus cyprinella* (Cuvier & Valenciennes); European carp, *Cyprinus carpio* L.; common sucker, *Catostomus commersonii* (Lacépède); channel cat, *Ictalurus punctatus* (Rafinesque); and black bullhead, *Ameiurus melas* (Rafinesque). It should be noticed that this group of fishes depend upon the bottom of the stream for their food materials, which include detritus and the predominants of the bottom community.

The following influents: Common shiner, *Notropis cornutus* (Mitchill); river chub, *Hybopsis kentuckiensis* (Rafinesque); calico bass, *Pomoxis sparoides* (Lacépède); chub sucker, *Erimyzon succetta oblongus* (Mitchill); little pickerel, *Esox vermiculatus* Le Sueur; top minnow, *Fundulus notatus* (Rafinesque); pirate perch, *Aphredoderus sayanus* (Gilliams); long-eared sunfish, *Lepomis megalotis* (Rafinesque); green sunfish, *Lepomis cyanellus* Rafinesque; Johnny darter, *Bolesoma nigrum* (Rafinesque); large-mouthed black bass, *Micropterus salmoides* (Lacépède) are also important.

The large rivers comparable to the Illinois were not studied by the writer but the bottom communities studied in this paper constitute one layer of the small river climax described by Thompson and Hunt ('30) in terms of fishes.

Large Rivers

Viviparus Mud Bottom Association

The *Hexagenia-Musculium-Limnodrilus* Community was the final stage of development upon mud bottom studied. Since the Sangamon River is a typical small river, the Illinois River near Peoria, studied in 1913-1915 (Richardson, '21b), before the effect of pollution became evident offers an interesting possibility of differences between the climax in the small and large rivers. The Illinois River is a mature stream which has a large flow of water. The dominants of this community include all the fish species found in the small rivers and their ecological equivalents in the form of closely related species.

This bottom layer community which is subordinate in the complete community in 1914 was characterized by the prevalents *Musculium transversum* (Say), *Campeloma subsolidum* Anthony, *Viviparus contectoides* W. G. Binney, *V. subpurpureus* (Say), *Lioplax subcarinata* (Say), *Pleurocera* sp., *Ammicola emarginata* Küster, *Musculium jayense* (Prime), *Pisidium* sp., *Valvata* sp., *Hexagenia* and chironomid larvae (large red), chironomid larvae (small), small Oligochaeta, small leeches, *Palpomyia* sp., and caddis fly larvae.

Richardson ('29) in discussing the competitive relations among the important animals of this community states that it cannot be said that competition for food has been at any time an important influence on numbers.

"In so far as these groups use the same food, namely, the living bottom plankton and bacteria and the settled plankton and fine organic detritus, they are competitors in a general sense, but by reason of the practically limitless amounts of these materials available, at least in the reaches of the Illinois River with less current, competition for food is practically non-existent in actual practice, although all three groups (Tubificidae, Sphaeriidae, and Chironomidae) have often in recent years been found associated in large numbers over the same bottom area."

The gastropod molluscs, because of their large size and their habit of taking in practically everything that lies in their path as they crawl along the river bottom over encrusted sticks, stones, or dead shells, exert a very important effect upon the other constituents of the community. If these forms once become dominant in an area, this fact seems to give them a more or less permanent and, if abundant, often almost undisputed foothold. This undisputed possession of the habitat may be due to several factors. Many of these gastropods are quite capable of ingesting the eggs of many of the insects. Owing to their habit of secreting a slimy tract along which they move they may shut off oxygen from such burrowing forms as Tubificidae, Chironomidae, etc. They may also smother the smaller forms by sheer weight. Richardson believes that the Sphaeriidae are more able to compete with the gastropods in such a situation because the young are born alive with a fully formed shell and are larger than the type of food usually chosen by the snails. Unionidae are not so important in the mud sere although there are a few forms which reach a certain degree of abundance. As a general rule however, these forms are ones which have migrated into the muddy area after they have reached some size, since the young are quite often smothered if they are dropped on the mud floor.

Sand Bottom Pools

Numerous dredge hauls have been made in sandy pools but they yielded no animals. Sand is rarely a stable habitat; many sandy areas will never possess communities because of constant shifting. Floods often cause complete changes of bottom at any given point.

Chironomus sp.—(*flavicingula*?) Sand Bottom Community

On the newly deposited sand near the headwaters of the stream very little if any life can exist, however *Chironomus* sp. (*flavicingula*?) is the first animal to appear (table XII) upon such an area wherever the sand remains

TABLE XII. *The distribution of the animals over the sand bottom as found at the various stations along the stream*

a (Fox Run), b (Deland), c (Deland), and d (Monticello) are stations in Goose Creek. e (Monticello) is located in Camp Creek, and f (White Heath) and g (Monticello) are in the Sangamon River. Station a is the youngest stage of the physiographic succession and g is the oldest stage of the same succession.

	a	b	c	d	e	f	g
* <i>Chironomus plumosus</i>	19	5	9	2	.		
<i>C. sp. (flavicingula ?)</i>	15	27	45		4		
<i>C. sp. (fulviventrís ?)</i>		27		3			
<i>Orthocladíus sp.</i>		12	5		5		
<i>Hydropsyche sp.</i>			1	25	1	0.3	
* <i>Hexagenia bilineata</i>			8	25	8		4
* <i>Palpomyia sp.</i>				1			
<i>Gomphus externus</i>				1			
<i>Tanypus sp. no. 1</i>				1			
<i>Tanypus sp. no. 2</i>				1			
Tabanidae (Larvae).....					4	2	
* <i>Musculium transversum</i>					4	0.3	0.2
<i>Taeniopteryx nivalis</i>						0.9	
<i>Baetisca sp.</i>						0.3	
<i>Strophopteryx fasciata</i>						0.3	
<i>Gomphus descriptus</i>							0.2
<i>G. spiniceps</i>							0.2

* These forms are also found in the quasi-experimental areas.

stable. It far outnumbers any of the other members of the community although at times *C. plumosus* attains a fairly important place. Very few other animals are able to maintain themselves upon this type of bottom. Associated with *Chironomus* sp. (*flavicingula*?) are: *C. sp. (fulviventrís ?)* and *C. plumosus*, especially where mud is present. The sand and gravel soon become covered with a growth of filamentous algae, which provide food, either in the form of living material or as detritus after it begins to disintegrate, and hiding places for various species of animals. *Chironomus* sp. (*fulviventrís ?*) and *Orthocladíus* sp. are prevalents of such a community. Estimates of three hundred individuals of *Orthocladíus* sp. per square meter upon some of these areas were considered low. *Cambarus virilis* Hagen is also a member of this community. This algal-covered sand, with its animal population also attracts certain fishes, for example the green sunfish, *Lepomis cyanellus* Rafinesque, which is found in such streams. In favorable seasons enough detritus and organic matter may accumulate upon the sand to attract the burrowing mayfly nymphs of the genus *Hexagenia*, the burrowing dragonfly nymphs, *Gomphys spiniceps* Walsh, and *Macromia illinoiensis* Walsh, and *Limnodrilus* sp. This community occupies all the sand bottom of Fox Run

(with the exception of the newly deposited sand) and in the lower deeper parts of Goose Creek (table XII). Where the rate of flow of water is slow and the volume is not great, the typical fishes of this community are the same as those of the early stage of the mud bottom sere with the addition of the silver-mouthed minnow, *Erinnyson sucetta oblongus* (Mitchill). The development of this *Chironomus* sp. (*flavicingula*?) community has not been thoroughly studied. It is evidently replaced by the *Musculium-Lampsilis* Sand Bottom community when the water remains permanent for a few years.

Musculium-Lampsilis Bottom Community

The *Musculium-Lampsilis* Community occupies the lower portions of Goose Creek, Camp Creek from Seymour to the Sangamon, and the Sangamon River wherever the sand has not been moved for some time. The depth of water varies from eight inches to three or more feet, and the stream may be from six to fifty feet in width. The two most prevalent species are *Musculium transversum* Say and *Lampsilis ventricosa* Barnes.

Creeks in which no mud has been deposited upon the sand have a population composed almost entirely of the finger nail shell, *Musculum transversum* Say. In Mansfield Creek in 1928 (table XII) these animals were found near its mouth, but nothing else for four miles above and similarly again some ten or fifteen miles above the mouth. As a further example in a pool formed by a rock outcrop in Stony Creek, near Muncie, Illinois, this species was very abundant on the sandy portions of the pool, but absent where mud occurred. The mud was occupied by *Hexagenia* nymphs and burrowing dragonfly nymphs (*Macromia illinoiensis* Walsh). This condition is similar to that found in Decatur Lake.

Lampsilis ventricosa Barnes occurs in the upper portions of Goose Creek in as little as four inches (10 cm.) of water and migrates into the deeper pools with decreasing depth. It sometimes burrows into the stream bottom as the water recedes. As a result of being completely aquatic it is very scarce in the smaller streams; only scattered specimens have been found in the lower four miles of Goose Creek.

In the rivers and larger streams these sand areas have much larger populations which exhibit a larger number of prevalents as well as a larger population. *Lampsilis siliquoides* (Barnes), *Cyclonaias tuberculata* Raf., *Pleurobema coccineum* (Conrad), *Quadrula metanevera* Raf., *Q. quadrula* Raf., *Q. pustulosa* (Lea), *Elliptio dilatatus delicatus* (Simpson), *Fusconaia flava* (Raf.), and many other species of mussels, in addition to *Musculium transversum* and *Lampsilis ventricosa*, are found on the sandy areas even when mixed with pebbles. The pink heel splitter, *Proptera alata megaptera* (Raf.), and the white heel splitter, *Lasmigona complanata* (Barnes), occur in greatest abundance on pure sand, or sand mixed with mud. The snail *Pleurocera* sp. occurs in this type of habitat.

From a study of Thompson and Hunt's paper ('30), it will be seen that the dominants and influents of the communities are essentially the same as those found in the *Hexagenia-Musculium-Limnodrilus* mud bottom community. *Pomoxis annularis* Rafinesque and *Micropterus dolomieu* (Lacépède) are found here instead of their ecological equivalents *Pomoxis sparoides* (Lacépède) and *Micropterus salmoides* (Lacépède).

The *Musculium-Lampsilis* Community is the highest stage in development of the sand bottom and represents the sand faciation of the climax in large streams. Much of the habitat occupied by this community appears to be very stable. Some communities under observations have not changed so far as composition is concerned during five years of observation. That they have existed in practically the same condition for a much longer period is evidenced by the fact that the zoological classes of the University of Illinois have collected in the same region for some years and the results of their efforts always have been practically the same.

For the most part the inhabitants of the more stable areas of sand are types which help to stabilize their habitat. Thus a mussel by its thick shell and its strong muscular foot tends to prevent the washing away of sand to a considerable extent and in this way tends to make permanent areas which before the invasion of the mussel were constantly being shifted from place to place. Even though Unionids tend to stabilize their habitat, many of them are swept from their surroundings by the current, as is indicated by the concentration of great numbers of individuals in the more rapid portions of the stream.

Hexagenia sp. and other mud inhabitants invade the sand bottom only when a small amount of silt or detritus has been deposited upon the sand. Where detritus is deposited, the invasion of *Hexagenia* is due to the effect of other organisms.

DISCUSSION

This study has strongly suggested the existence of but a single major community and its developmental stages and variations or faciatiions. The development of communities (fig. 7) in the pools formed by dams demonstrates this and forms a basis for the interpretation of the various fragments of a community found in pools of the Sangamon River and its tributaries.

The writer is convinced that any attempt to bring the stream physiographic history into play along the lines indicated by Shelford ('11 and '13, Chapter 6), confuses rather than clarifies an understanding of community relations in the streams under consideration at least.

Shelford ('13) described the relation of certain communities to the development of some streams located near Chicago. The succession of communities to be found at a fixed point from time to time as a stream grows older is termed physiographic succession, which according to present concepts is erroneous. The small streams studied by Shelford presented a series of communities; or better on the whole, a series of slight modifications of the

same community characterized by the addition of species as the observer passes from the source to the mouth of the small stream.

The series presented by Shelford ('11, '13, chapter 6) for the small streams flowing into Lake Michigan was clearly stated only for fishes. There was one fairly distinct group of invertebrates where these streams were intermittent, and another in the parts of the largest permanent stream. The principal fact brought out is the existence of faciations of the intermittent stream community. Turning to larger streams, it is made evident by this study and supported by the work of others (Eddy, '34, Thompson and Hunt, '30), that distinctly different communities are not readily distinguished in a lengthwise study of a stream as they are in the case of a series of temporary invasion groups which may be washed out by the next high water. These temporary invasion groups may serve, however, as an aid in the study of the early stages of succession in stream communities. The mixing of phenomena working thousands or even millions of years, with those requiring ten to twenty years can hardly clarify or solve the problem.

Shelford considers that there are but two main types of stream communities typified by (1) those of rocky rapids and (2) by mud bottomed pools. He regards fishes as the most important dominant of the latter. Certain semi-pool aggregations are considered as ecotones between the two. He has termed the rapids community a quasi-climax, but states that the term might equally well be applied to the lichen community on a granite boulder. He states the relations of the climax in the following terms (personal communication) :

"The criteria for climax communities are (a) the constituent organisms exercise a considerable degree of control over the habitat, (b) the controlling reactions and co-actions tend to maintain the habitat and community in a climax condition, (c) communities undergo development and during this process a series of changes take place in the habitat and in the community, (d) climaxes exist under stable physiographic conditions. In streams large stretches of climax can occur only in large streams at base level throughout, but obstructions, bending, etc., which provide pools in which silt deposits are small and a stable mud bottom occurs, afford examples of climax, chiefly as relatively small fragments. The chief dominants are fishes, carp, buffalo, sturgeons, cat-fishes, suckers, gizzard shad, etc., which feed on bottom detritus and vegetation keeping the channel essentially clear of the latter. The striking effect of fishes of this type is well illustrated by the work of Cahn ('29). Faciations of the climax occur in streams of all sizes large enough to support several species of fishes of the dominant types. The Sangamon River near Mahomet, Illinois, approaches the minimum size in which a climax stream community may be expected to exist."

The confusion of biotic succession with so called physiographic succession of earlier writers (Cowles, Adams, Shelford) together with the practice of separating plankton, invertebrate bottom fauna, and fishes in investigational projects has retarded the clarification of freshwater community phenomena and the description of freshwater climaxes. This study indicates that two of the four or five types of habitats and communities enumerated on page

are well developed. These are (1) the mud-bottomed pool climax type essentially without rooted vegetation and with insects and molluscan predominants, and with fishes as the most important dominants, (2) the sand-bottomed communities with molluscan predominants, and in the main the same fish dominants.

The community in which the molluscs are predominant appears to be quite distinct from the mud bottom type. The taxonomic composition of the fish population over the sand bottom and of the bottom fauna is essentially about half different. Classification of this community as a seral stage seems best. The bottom animals cannot hold the sand in place, though mussels help to some extent, and the fishes cannot dominate the bottom as they do in muddy pools. The evidence in hand indicates that sand which is not seriously displaced over a period of several years during a dry climatic phase, develops from the *Chironomus* sp. stage to the *Lampsilis-Musculium* stage, but evidently can progress no further by the effects of organisms but must await changes in the stream conditions before progressing to another stage. The only biological factor which possibly operates to make the sand have the properties of mud is the accumulation of organic detritus.

The following diagrams show the size series and the biotic development series:

Communities		
Artificial lakes	Mud-bottomed pools	Sand-bottomed pools
<i>Chironomus plumosus</i> Societ	<i>Chironomus-Chironomus</i> (<i>fulviventris</i> ?) Societ	<i>Chironomus (flavicingula</i> ?)- <i>Chironomus</i> Societ
<i>Hexagenia-Musculium</i> Society	<i>Hexagenia-Musculium-</i> <i>Limnodrilus</i> Society	<i>Musculium-Lampsilis</i> Society
Stream Size Series		
Small creek	<i>Chironomus (flavicingula</i> ?)- <i>Chironomus</i> Layer Societ (Sand)	
Large creek or small river	<i>Musculium-Lampsilis</i> Layer Society (Sand)	
Creek and river pools	<i>Hexagenia-Musculium-</i> <i>Limnodrilus</i> Layer Society (Mud)	
Large rivers	<i>Hexagenia-Chironomus-</i> <i>Viviparus</i> Society	

The first diagram shows three phases of the short biotic sere which are hardly distinct but represent different facies and faciatiions of the same major community, *i.e.* the climax and its developmental stages with differences brought about by the loss or addition of one or two species.

The second diagram represents the change in the predominant communities as one passes from a small creek to the Illinois River. The sand in-

habiting communities are shown in series because they predominate in these small streams. As the stream gets larger, mud bottom predominates and there is a change from *Musculium-Lampsilis* to *Hexagenia-Musculium-Limnodrilus* as the predominant type.

The evidence at hand indicates that one large community with its developmental stages occupies the relatively still waters of the Illinois River (a nearly base level stream) where all the more important species are represented. From the pools of this stream, a census of the fishes and invertebrate bottom community constituents from pool to pool as one proceeds toward the smallest tributaries reveals a few substitutions of equivalent species, as for example of *Musculium*, but mainly a dropping out of constituents. There are also a few additions of species peculiar to streams of particular size, which make this biome probably divisible into associations which show various faciations. To verify this further knowledge than that which can be pieced together from the separate works of Eddy, Thompson and Hunt, and the writer, regarding life histories and specific identification of the chironomids will be necessary as well as a more careful correlation of plankton. However, the progress to date indicates that community development forms the guide to the interpretation of classification.

SUMMARY

1. Quantitative samples of the bottom inhabitants of quasi-experimental conditions represented by artificial pools and by the streams of central Illinois were made with the Peterson bottom sampler.

2. Three definite successional stages in the development of bottom communities were found on the bottom of these artificial lakes, characterized by *Chironomus plumosus* (on the youngest stage), *Procladius* sp. no. 2, *Hexagenia* sp. and *Musculium* sp. (on the oldest stage), in the order named. *Limnodrilus* sp. and members of the Ceratopogonidae become extremely abundant where much organic material is deposited, but are not considered to be typical in the succession in these reservoirs. In all of the developmental stages fishes must be considered as the most important dominants of the community.

3. The communities existing in the streams of central Illinois are characterized by the same invertebrate dominants as those which develop upon the bottom of the artificial lakes. The *Hexagenia-Musculium* mud bottom community is considered climax for streams of the size of the Sangamon River. In mature streams (the Illinois River), the *Hexagenia-Musculium-Viviparus* Community is climax.

4. Biotic succession constitutes a guide to the interpretation of the classification of freshwater communities.

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A QUANTITATIVE DETERMINATION OF CHITIN DESTROYING MICROORGANISMS IN SOIL

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A few workers have isolated from soils, organisms capable of dissolving chitin (Benton, '35; Jensen, '32; Johnson, '32), but as far as can be found from the literature examined, there is no report on their abundance. The most extensive study, that of Benton, concerned itself with morphological and qualitative ecological aspects of the subject.

Chitin is the name originally used by chemists to designate the hard covering of insects. The original term, "fungine," which referred to that derived from plant sources, Basidiomycetes, was used by the discoverer Braconnot in 1811, but this word has been superceded by "chitin." There is evidence that there is one chitin, whether it is from animal or vegetable source. A few possible exceptions have recently been reported in certain fungi and marine worms. The chitin from various portions of the insect is chemically identical (Campbell, '29; Irvine, '09; Webster, '09).

Chitin is abundant in nature. It forms the chief constituent of the exoskeletons of arthropods and is abundant in the Eumycetes, particularly the Basidiomycetes. Morris ('20, '22) records the following numbers of arthropods in one acre of soil to a depth of nine inches on two fields at Rothamsted, England. These are twelve-month averages.

	Unmanured plot	Plot receiving farmyard manure
Insects	2,474,700	7,727,300
Millipedes	596,000	1,367,000
Centipedes	215,400	208,700
Symphyla	64,000	215,500
Mites, ticks	215,400	531,900
Spiders	20,200	20,200
Woodlice	33,700	80,800

Monographs by Russell ('27), Waksman ('32), and Shelford ('29) have accumulated considerable data on the abundance of insects and other arthropods in soil. The writers have not investigated the accuracy of the method used by Morris. At least the data do show a very large chitin-bearing fauna, and the error of the method, if any, would appear to result in an understatement of the actual abundance. The abundance of fungi in soil has been treated by Brierly (Russell *et al.*, '23) and by Waksman ('32).

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Various structural formulae have been reported for chitin. The most generally accepted empirical formula is $C_{32}H_{54}N_{10}O_4$. On hydrolysis it yields glucosamine and acetic acid, the former of which, on further hydrolysis, gives rise to NH_3 , CO_2 and H_2O . However, this is a very slow process as compared to the decomposition of many other organic compounds. The properties of pure chitin may be summarized as follows (Campbell, '29; Irvine, '09; Webster, '09).

1. Chitin is hydrolyzed by (a) concentrated mineral acids to glucosamine and acetic acid, (b) concentrated KOH or NaOH at high temperatures ($160^\circ C.$), which transforms it to chitosan and acetic acid, with no change in appearance.
2. Sodium hypochlorite or 5 per cent chlorine oxidizes it and dissolves it at room temperature.
3. Chitin is not soluble in water, alcohol, ether, dilute acids or dilute or concentrated alkali at moderate temperatures.
4. When treated with I, KI, and H_2SO_4 , it gives a brown color reaction.
5. Physical determinations show it is laevorotatory, index of refraction is $1.525 \pm .005$, and specific gravity is 1.40.
6. It is not digested by mammals.

EXPERIMENTAL

Soil samples were collected in sterile bottles except a few samples of alkali soil from the intermountain region of the western states. These samples were found in the laboratory and had been there several years. The source of all samples together with the moisture content and pH are indicated in table I.¹ All samples were from the vicinity of Prescott, Wisconsin, near the mouth of the St. Croix River, unless otherwise indicated.

The approximate numbers of chitin decomposing bacteria in the soils capable of growing in the medium used were determined within a few days after collection by the method of decimal dilutions in replicates of ten according to the method of Halvorson and Ziegler ('33). Obviously, plating methods with ordinary media could not be used, for chitin destroying bacteria could not be differentiated from others. Plating on agar media into which finely divided chitin was incorporated and counting colonies with enzymic zones suggested itself. Experience of one of the authors with cellulose agar plates ruled out this method. He found, like Benton ('35) with chitin agar, that such plating media are useful for isolation of organisms. But, in his hands at least, they are useless for quantitative plating. The dilution method, especially adapted for counting physiological types on selective media from the mixed soil populations, has been used by Löhnis ('05), Millard ('11), and others, but in all experiments known to the authors because only a few tubes per dilution were used, or because of wrong calculations of the data,

¹ We are indebted to Mr. E. J. Ordal for making pH determinations. He used a glass electrode.

the mathematical error is so great as to vitiate any conclusions. Cutler, Crump, and Sandon ('22), Perey ('22), Sandon ('28) and Dixon ('28) have used a method similar in principle, with fewer replicates but in a series of 1:2

TABLE I

Sam- ple no.	pH	Factor (Gram air dry soil per gram moist soil)	Source
1.	6.07	0.435	Alfalfa field.
2.		0.860	Near deciduous tree stump on grass land.
3.	5.40	0.856	Mixed woods, growing wild.
4.		0.929	Uncultivated grass land on hillside near Lake St. Croix.
5.		0.858	Sandy shore line on Lake St. Croix.
6.	6.5	1.000	Sandy bluff along Mississippi River.
7.		0.984	Clay loam from hillside near cultivated field.
8.		1.000	Sandy soil from Mississippi river bottom.
9.		1.000	Sandy soil between Mississippi river bank and railroad track.
10.		0.980	Clay and sandy soil near Mississippi river.
11.		0.995	Clay and sandy soil on roadside near Mississippi river.
12.		0.824	Black fertile loam near an old sunken well on cultivated land.
13.	5.3	0.924	Clay soil from slope near road.
14.*	5.07	0.887	Woodland used for pasture.
15.*	5.90	0.956	Cultivated soil.
16.*	8.40	0.883	Meadowland usually flooded in spring and summer (near LaCrosse, Wisc.).
17.*	7.3	0.805	Meadowland usually flooded in spring and summer (near LaCrosse, Wisc.).
18.*		0.980	Lower portion of bluff, much vegetation, near LaCrosse.
19.*		0.731	Along shoreline of Pine Creek, Houston Co., Minn.
20.		0.750	Shore line debris beneath mats of algae, unit 3 of Bear River Refuge, Utah. Contains many snails (8-11-33).
21.		0.734	Soil from beneath body of male green-winged teal that had died in the fall of 1932. Willard Spur, Utah (8-12-33).
22.		0.767	Soil from beneath body of a mallard duck that had died in the fall of 1932, Willard Spur, Utah (8-12-33).
23.	8.4	0.748	Soil from beneath body of pintail duck that died in the fall of 1932 (8-12-33).
24.	8.2	0.738	Soil from beneath body of shoveller that died in the fall of 1932 (8-12-33).
25.		0.727	Soil from beneath body of a coot that died in the fall of 1932 (8-12-33).
26.†			Garden soil from greenhouse, Minneapolis.
27.†			Garden soil, Minneapolis.

* Slightly frozen when sampled.

† Moisture determinations not made.

dilutions, to count soil protozoa, and definite conclusions may be drawn from their work. Likewise Bristol-Roach ('27) and others (Skinner, '32) have used dilution methods for counting soil algae and have definitely established a large number of algae capable of multiplying as an important part of the

soil flora. But little work has been done by the dilution method with an adequate number of replicate tubes to count physiological groups of soil organisms, although the method is ideal for such purposes.

The method is simple. A selective medium is used. For the present work the medium was the one employed by Johnson: 0.03 per cent of each of three salts, NaCl, $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ and K_2HPO_4 , and a strip of chitin prepared by the method described by Benton added to each tube so that it was partly submerged. Decimal dilutions were made and 10 tubes were inoculated with 1 cc. of each dilution. A separate pipette was used for each manipulation, an obviously necessary precaution in all quantitative plating, but one often omitted. After three months, the tubes showing any dissolution of the chitin were counted, and the number of chitin destroying microorganisms was estimated from the tables of Halvorson and Ziegler ('33). A correction for moisture was made so that all figures are expressed on the air-dry basis. The limits of "reasonable accuracy" are also given. These figures (table II)

TABLE II

Sample no.	Most probable number per gram of air dried soil	Limits of reasonable accuracy (97%)
1.	Over 52,800	
2.	26,700	11,870- 66,750
3.	14,000	6,020- 35,000
4.	24,700	19,770- 61,750
5.	13,900	6,170- 34,750
6.	288	129- 720
7.	3,150	1,400- 7,850
8.	13,300	5,800- 33,250
9.	11,300	5,020- 28,250
10.	80,000	35,550- 200,000
11.	350,700	155,760- 876,750
12.	1,432,000	636,400-3,580,000
13.	10,600	4,250- 26,500
14.	513,900	228,400-1,284,750
15.	398,000	176,880- 995,000
16.	183,200	81,420- 458,000
17.	285,700	126,970- 714,250
18.	234,600	108,710- 586,500
19.	960,300	426,800-2,400,750
20.	12,200	5,420- 30,500
21.	Less than 149	
22.	1,310	580- 3,270
23.	Less than 147	
24.	149	66- 370
25.	Less than 149	
26.*	1,280,000	568,800-3,200,000
27.*	2,880,000	1,290,000-7,200,000

* Moist soil basis.

show the number of organisms per gram of dry soil which would be obtained in 97 per cent of the cases from the data observed.

We also desired to know whether the property of dissolving chitin is common to many of the soil organisms. To obtain this information, soil was

plated out in high dilutions on soil extract agar for bacteria and on peptone-glucose acid agar for molds (Fred and Waksman, '28). After two weeks, colonies were picked at random and inoculated into the chitin medium. In one case, 291, and in two other cases, 250 colonies of bacteria were inoculated. The percentage of chitin dissolving bacteria was estimated. Likewise, a number of molds were picked from acidified glucose peptone agar, and the number of them dissolving chitin was determined. When it is indicated that colonies were picked at random, it means either that all colonies on a plate were picked or that all those in a portion of the plate were picked. This was done to minimize the danger of picking only conspicuous colonies.

One thousand and eighty tubes of chitin media were inoculated for the soil counts, but only 810 were used in determining the numbers, as Halvorson and Ziegler's tables are for three dilutions of 10 replicates each. Eight hundred ninety-one tubes of chitin media were used in testing for chitin destruction by isolated bacteria, actinomycetes, and molds.

The counts of chitin decomposing organisms expressed on the basis of numbers per gram of air dried soil are given in table II, together with the limits of reasonable accuracy. The total counts of organisms by the plate method were not determined, with the exception of samples 26 and 27.

In the first sample of soil plated, which was garden soil, 291 colonies were picked at random, of which about 40 per cent were actinomycetes. Only 24 dissolved chitin; all of these save two were actinomycetes. No dilution counts of chitin destroying bacteria or of total plate counts were made from this soil. The second sample, a greenhouse soil, no. 26 of the table, gave by dilution method a count of 1,280,000 chitin destroying bacteria per gram of moist soil, and a bacterial count of 240,000,000 per gram (average of 6 plates). The number of colonies picked was 250, of which 83 were actinomycetes. Only one of the 250 colonies picked at random decomposed chitin. It was an actinomycete. A third sample, a dry garden soil, no. 27 of the table, gave by the dilution method a count of 2,880,000 chitin destroying bacteria per gram and a bacterial count of 360,000,000 per gram (average of 10 plates). The number of colonies picked was 250 of which 112 were actinomycetes. Four out of the 250 colonies picked at random dissolved chitin. Three of these were actinomycetes.

Of the one hundred molds isolated at random from several different soil samples, 42 dissolved chitin. The following genera were identified: *Aspergillus* (2 strains), *Mucor* (6), *Penicillium* (2), *Absidia* (1), *Trichoderma* (4), *Fusarium* (1), *Gliocladium* (2), *Thamnidium* (2). Those identified but which were unable to dissolve chitin were *Aspergillus* (7 strains), *Fusarium* (3), *Penicillium* (6), *Cephalosporium* (6), *Alternaria* (2), *Cunninghamella* (2), *Monilia* (1), *Hormodendron* (1). It is noteworthy that although Phycomycetes are unique among the molds in that none of them decompose cellulose (Waksman, '32), several of the molds which were found to decompose chitin actively were Phycomycetes.

DISCUSSION

In checking the tubes which showed chitin destruction, it was noted that in the higher dilutions of all soils except the dried alkaline ones, most of the tubes contained true bacteria rather than molds or actinomycetes. It is thus apparent that (assuming, as seems justified, the medium used to allow development of at least as large a proportion of the chitin destroying molds and actinomycetes as of true bacteria) the soil has a larger population of true bacteria than of molds or actinomycetes which are capable of chitin destruction. The findings here were the same in all of the 21 undried soils, i.e., chitin dissolving Eubacteriales were more numerous than molds or actinomycetes. Such uniformity is significant.

Less significant, but worth mentioning, is the fact that when three soils were plated in soil extract agar and colonies picked and planted in the chitin medium, most of the tubes which showed chitin destruction contained actinomycetes. Benton ('35) found that some of the strains of her chitinivorous bacteria from soil exhibited a "practically invisible growth" on beef peptone agar. Possibly the majority of chitin decomposing Eubacteriales fail to grow, or grow so poorly as to be practically invisible on soil extract agar as well, thus explaining why chitin destroying actinomycetes outnumbered true bacteria when picked at random from poured soil extract agar plates.

Almost one half of the strains of molds isolated dissolved chitin more or less, but in most cases the action was slower than when carried out by true bacteria even on the portion of the strip of chitin above the liquid in the tube. The action of most of the actinomycetes was also slower than that of the true bacteria, as Benton found. The Phycomycetes were numerous among the chitin destroying molds, and especially rapid in their dissolution of chitin, which is quite contrary to their well known lack of cellulose dissolving power. Possibly this is related to the fact that the fungi parasitic on other fungi and many of those on insects are Phycomycetes.

SUMMARY

A large number of chitin destroying microorganisms were counted, by means of the dilution method and selective liquid media, in 26 soils. The counts varied in normal soils from 288 in a dry sand bank along the Mississippi river to over one million per gram in a fertile cultivated black loam and in garden soils. In every case, few of the organisms responsible for chitin decomposition were molds, less than half actinomycetes.

Of six alkali soils, stored for more than two years, three still had a small population of chitin dissolving microorganisms, all being actinomycetes.

Very few of the bacteria (Eubacteriales and Actinomycetales) which developed in 14 days on soil extract agar plates from soil dilutions were able to dissolve chitin when inoculated into selective media. Of these nearly all were actinomycetes.

Slightly less than one half of the molds which developed on peptone-glucose acid agar plates from soil were able to dissolve chitin.

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RELATIONSHIP OF SOUTHERN CEDAR GROWTH TO PRECIPITATION AND RUN OFF

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Interest in tree ring studies by the Douglass method might be said to have focused principally on four fields of contact:—archaeology, botany, meteorology, and astronomy, although, as a new science, dendrochronology contacts, uses, and eventually may add some data to the libraries of accumulated knowledge catalogued even for other sciences. Since he began the study in the first years of the twentieth century, Dr. Douglass' primary interests have been the reflection of astronomy and meteorology in tree growth: the effect of terrestrial conditions upon the annual increment of trees over a known recent period, and from that, the record of wet and dry periods as indicated by the tree ring records which extend centuries farther into the past than any human records. Definite identification of tree ring patterns covering sequences of years was found to be possible, and by matching the outer sequences of rings of older trees onto the inner sequences of modern specimens, by what has been called the "bridge method," a record was compiled in which the year of every narrow and every wide ring was known, and onto which the growth record of roof beams from prehistoric Southwestern pueblos might be matched and their cutting dates thereby ascertained. This development was of great importance to southwestern archaeologists, for now instead of arguing over the probable century in which any pueblo was built, a beam from its ruins can be examined at the Douglass' laboratory and the year in which the tree which made the beam was cut may be identified.

CORRELATIONS OF WESTERN PINES, SEQUOIAS, AND PRECIPITATION

But whether the end in view be the date of a ruin or correlation with sun-spot cycles, the basic material is biological and much of our investigation, as that of the present paper, must be concerned with the qualitative and quantitative relationship of tree growth to various meteorological and geographic factors.

Although perhaps the most widely known tree ring work is that done on pines in the American southwest, Dr. Douglass has tested trees and their reflection of weather fluctuations in many other parts of America and Europe. The California *Sequoia washingtonia* proved to give good cross-dating in almost every tree, although these trees produce annual rings that average less variation from year to year than do those of the pines. In North Germany

and near the Arctic Circle in Sweden the pines have been cross-dated. Pines in New England and in the Ozarks have been tested by Dr. Douglass but no extensive work was undertaken on middle western or on southern trees until the University of Chicago asked the writer to work on this task in the spring of 1934. Although the primary interest was the eventual dating of the mound builder remains, an archaeological problem, that question could not be broached without preliminary studies to determine which trees best cross-dated among themselves and which carried records long enough that a master chart might be pieced together to extend far enough into the past to pick up the records of ancient roof beams, wall poles, mound stair facings, fire wood, or grave coverings.

In this work pine, many varieties of oak and of cedar, and hickory, cucumber, gum, and poplar from east Tennessee and from west Kentucky were examined, both by cross section and by borings extracted with the increment borer commonly used by foresters. Pines, white oaks, red cedar and *Thuja occidentalis*, showed the greatest sensitivity in ring growth and the longest growth records, as well as the widest distribution both in modern groves and in specimens preserved either as partially decayed wood or as charcoal in Indian mounds. Of the three trees, the red cedar, *Juniperus virginiana*, offered the best possibilities for the work of dating. Second to the cedar may be rated the white oak, *Quercus alba*.

As a master chart is used not only for dating but also for indicating the periods of drought and of abundant rainfall, correlation between modern precipitation and run-off and the annual growth rings of the species under consideration were necessary. Although the total of factors effecting tree growth and the exact effect of each of the known factors have never been determined, precipitation, soil conservation of water, temperature, evaporation, light, and soil composition are usually considered to be the most important determinants of growth.

Our work to date has been concentrated especially on the red cedar. To insure the greatest reliability possible, correlation of cedar growth, precipitation and stream run-off have been computed from a restricted rectangular area bounded by rainfall and stream gauging stations in eastern Tennessee.

Douglass reasoned that if widely separated trees in a uniform area show uniform variations for certain years over a long period, those variations must be due to the one common and continuous factor, climate. For the lower forest border near Prescott, Arizona, he found a correlation coefficient of 72 between pine growth and rainfall, after a conservation factor had been applied to the precipitation curves. For southern California the correlation between Redland pines and Lynche's rainfall indices was lower, but the resemblance of rainfall to tree growth curves was marked, especially in the minima. The correlation of sequoia, *S. washingtonia*, growth to rainfall at the nearest station, 200 miles distant, is only 28, a relationship probably real but low because of the distance and because of the fact that the water supply,

while still vital, is not as important a factor to the sequoias as to the Arizona pines.

SOUTHERN CEDARS

Although the western junipers tend toward being erratic in growth, due to the arid climate and lack of soil conservation of moisture, the southern junipers, popularly known as cedars, are not so stinted for water and hence carry readable records, sensitive to weather variations and not complacent.

The Virginia red cedar carries a long sensitive record although subject to double rings which, however, may be detected microscopically and hence not confused with nor counted as singles. At present we have a tentative cedar chart extending 600 years into the past. Dating of Indian mounds by means of this chart and its extension through addition of mound specimens which match the chart with their outer rings but whose inner record extends even farther into the past is expected within the near future.

Selection of specimens. For the correlations of cedar growth, precipitation, and run-off, 42 trees were selected from a roughly rectangular area above Coal Creek and below Arthur and New Tazewell on the Clinch and Powell rivers in Eastern Tennessee. Many other specimens from this area were cross-dated with the 42, indicating that the sample was adequately representative. This sample is small enough to be easily handled, but large enough to avoid errors dependent upon fluctuation of sampling in a small group. All specimens came from healthy, uninjured trees growing on slopes and bluffs. Increment borings from standing trees and V cuts and sections from cut trees were used.

Treatment of data. The standardized average size of ring for the group was taken as representative of the normal growth of that species for the weather conditions of that year in that district. In obtaining these averages, the individual specimens were prepared for measurement by clearing the surface with a razor blade cut. The individual rings were measured on a machine especially constructed for the purpose and a curve was drawn up for the growth record of each specimen.

As trees growing in different localities in a district grow at different rates, depending upon the difference in the norm of available growth factors at that spot, each tree has an individual normal growth rate from which the variations in annual precipitation or ground water cause it to fluctuate. Moreover, the red cedar shows a tendency to grow more slowly in youth than in middle age, and the growth records must be corrected for this before their reaction to weather fluctuations becomes clear.

To correct for age-growth variations, the measured record of each specimen is standardized; that is, it is brought to a base line of 100, the common base for all. Thus, when the standardized or corrected values are averaged for each year, individual idiosyncrasies are eliminated and one has a record of mean growth increment dependent upon contemporary weather fluctuations.

When trends in weather records or in tree growth are to be studied, tree growth and meteorological records are smoothed to eliminate extremes of local fluctuations from the curves. The smoothing formula which Dr. Douglass has found most applicable is the Hahn formula, concerning which he says, ". . . three successive (overlapping) fluctuations are merged into a substitute for the middle one by averaging the three, with double weight given to the second. It is this double weight applied to the original whose substitute is desired that differentiates this formula from a running mean of three" (p. 43, Douglass, '19, Vol. 2). When the Hahn formula is applied to the Tennessee tree growth, run-off, and precipitation curves, it is found that higher correlations appear between Hahned curves than between curves smoothed with any of the following conservation formulae: $\frac{1-1-1}{3}$, $\frac{1-1-2}{4}$,

$\frac{1-2-3}{6}$, and $\frac{1-3-5}{9}$ (figs. 1, 2).

The hydrologic data for but one station, Coal Creek, could be stretched to 34 years; consequently it was necessary to interpolate values beyond the short measured records of the outer two stations. Data for this was borrowed from engineers of the Tennessee Valley Authority who had computed the values in inches for hydrographic records. The last thirty-four annual rings of the cedars were measured for comparison. The measurements were reduced to a common base of 100 and the mean ring-size for each year computed. The Pearson correlation coefficient (Yule, '29), customarily used in such studies, was employed for correlations of these data, smoothed and unsmoothed, with the hydrologic data. Correlations were computed for the 22 year period of 1911-1932, excluding the year 1920 in precipitation correlations, for which year the data are erratic.

Results. The results of the correlations of cedar growth and precipitation and run-off may be seen in the table below. Cedar growth is here expressed in terms of precipitation and run-off for water years only. By use of these equations, the precipitation and run-off of the past may be computed in terms of cedar growth of the past, and the probable cedar growth of any one year may be computed in terms of the precipitation or of the run-off of that year, results in each case being probably exact to within the range of the standard error of that equation at least two-thirds of the time. The probable error is likewise listed.

It is noted that cedar growth and precipitation show slightly higher relationships when computed for water years than when computed for calendar years, while cedar growth and run-off show higher correlation for calendar year figures. This is to be expected, as the tree growth of the spring is largely dependent on the precipitation of the preceding fall and winter months, the run-off from which concentrates in spring freshets.

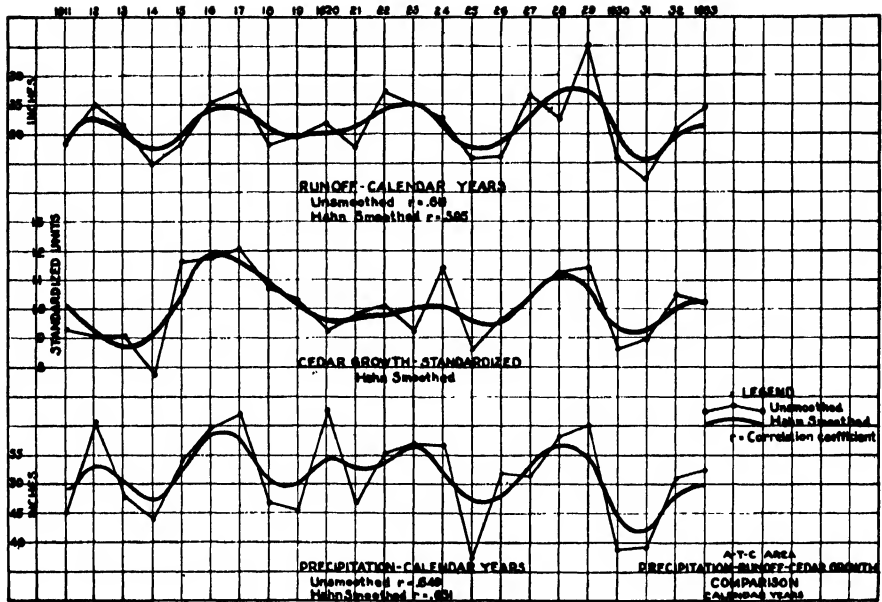


FIG. 1. A comparison of run-off, cedar growth and precipitation for calendar years 1911-1933.

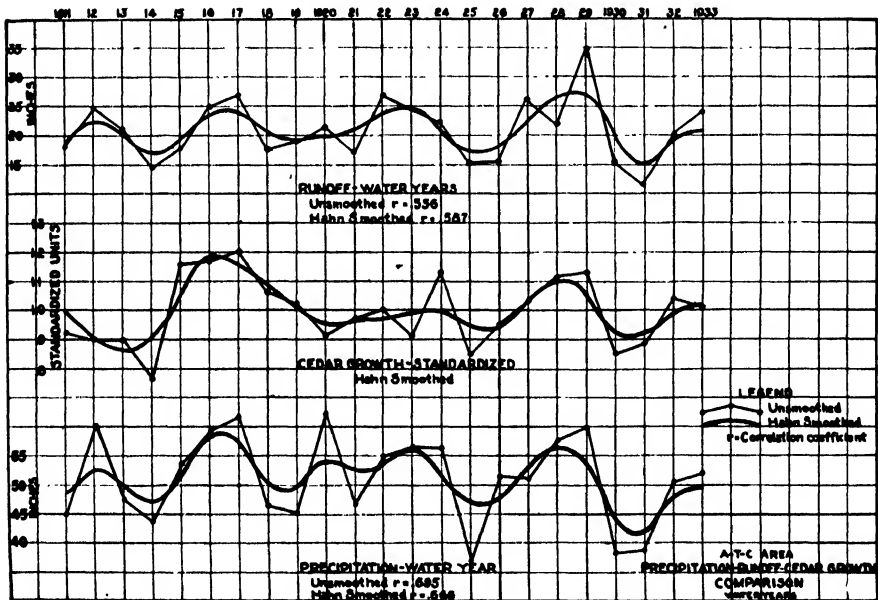


FIG. 2. A comparison of run-off, cedar growth and precipitation for water years 1911-1933.

TABLE I. *Correlations of cedar growth and precipitation (Sample of 42 Cedars) 1911-1932*

Calendar Year	Water Year	
Unsmoothed: $r = .6489$ $P = 33.15C + 17.94$ With SE_P of 4.66 in. $PE_P = 1.75$ in.	Unsmoothed: $r = .6949$ $P = 43.56C + 6.91$ With SE_P of 5.40 in. $PE_P = 3.64$ in.	Regression Equations $C = .011P + .443$ $SE_c = .086$ mm. $PE_c = .058$ mm.
Hahn Smoothed: $r = .6313$ $P_H = 25.83C_H + 25.37$ With SE_P of 2.59 in. $PE_P = 1.75$ in.	Hahn Smoothed: $r = .6664$ $P_H = 35.27C_H + 15.81$ With SE_P of 3.23 in. $PE_P = 2.18$ in.	$C_H = .013P_H + .358$ $SE_c = .061$ mm. $PE_c = .041$ mm.

Correlations of cedar growth and run-off (42 Cedars)

Calendar Year	Water Year	
Unsmoothed: $r = .6105$ $R = 25.19C - 3.49$ With SE_R of 3.87 in. $PE_R = 2.61$ in.	Unsmoothed: $r = .5562$ $R = 24.90C - 3.66$ With SE_R of 4.41 in. $PE_R = 2.97$ in.	$C_H = .012R + .744$ $SE_c = .098$ mm. $PE_c = .066$ mm.
Hahn Smoothed: $r = .5945$ $R_H = 19.39C_H + 2.13$ With SE_R of 2.14 in. $PE_R = 1.44$ in.	Hahn Smoothed: $r = .5865$ $R_H = 27.07C_H - .91$ With SE_R of 2.49 in. $PE_R = 1.68$ in.	$C_H = .016R_H + .669$ $SE_c = .066$ mm. $PE_c = .045$ mm.

 r = Pearson correlation coefficient C = Cedar growth P = Precipitation R = Run-off P_H = P Hahned R_H = R Hahned C_H = C Hahned SE = Standard deviation of regression line PE = Probable error

In comparing cedar growth and run-off curves, the correlations for unsmoothed data run somewhat higher for calendar years than for water years. In testing the correlations, computations were made for run-off figured from cedar growth over the period of 1904-1932. The computed unsmoothed figures for the calendar years with correlation of 61 per cent and the small probable error of 2.61 inches were, as an average 20.66 per cent in error from the actual figures. Water year unsmoothed precipitation and cedar growth shows a correlation of 70 per cent and probable error of 3.64 inches. In comparing actual figures on precipitation over the same period with precipitation figures computed by formula, the average difference was 10.13 per cent. For the calendar year, unsmoothed precipitation and cedar growth give a slightly lower correlation, 65 per cent \pm 3.14 inches P . Cedar growth and run-off figures for the same period of water years, unsmoothed, give a lower coefficient, 56 per cent \pm 2.97 inches.

The correlation of the Hahned calendar year run-off and cedar growth is slightly higher than for the Hahned water year and cedar. For the calendar

year, with a very small probable error of 1.44 inches, the computed run-off figures between 1904 and 1932 vary from the measured figures by an average of 12.47 per cent. It is to be noted that the correlations are consistently high, and that the standard errors, whether for expressing rainfall and cedar growth in terms of rainfall or of precipitation are low.

CONCLUSIONS

Of all the correlations tested for the group of 42 cedars, the relationship between unsmoothed cedar growth and unsmoothed water year precipitation proved to be the highest, $.6949 \pm 3.64$ inches P, or .058 mm. C, with a standard error of 5.40 inches P or .086 mm. C. This indicates a dependence of southern cedar growth upon precipitation to almost as high a degree as that of the southwestern pines.

It will be noted from figures 1 and 2 of cedar growth, precipitation, and run-off curves, that the crests of smoothed tree growth and precipitation curves fall on the same year, which is one year earlier than the crest of the run-off curves. A possible explanation for this situation is suggested.

Most of the precipitation of this area occurs during the winter, and it is this stored winter moisture plus the spring and summer rains which provides food for the spring and summer tree growth. The dry fall is not a growing period; consequently it is to be expected that the correlation between cedar growth and precipitation should be our highest. The fact that the maxima of the smoothed run-off curves comes one year later than the maxima of the smoothed precipitation and tree growth curves is probably linked with the fact that the soil water filters slowly through to the rivers and that the dry or wet conditions of the previous year influence the run-off of the present year. The minima of the cedar growth and run-off curves coincide. Thus: if the previous year has been dry and the soil consequently holds little storage of moisture, much of the precipitation of the present year is held in the earth while the rest seeps through quickly and becomes run-off for the present year. However, if the previous year has been wet and the soil already holds a high amount of moisture, some of the precipitation of the present year will run off at once but much of it will be held to slowly trickle through and consequently to augment the run-off of the succeeding year.

As an example, let us examine the years 1925 to 1929. 1925 was dry; minima appear in run-off, precipitation, and growth curves. 1926 brought much more precipitation, and cedar growth rose, but run-off remained quite low because the dry ground absorbed much of the available moisture. The excess ran off. In 1927, precipitation remained as in 1926, but tree growth raised slightly because of stored moisture, and run-off raised a great deal, for the same reason. 1928 was much damper in precipitation and trees grew well. The water year run-off fell but the calendar year rose, due to seasonal concentration of storms. In 1929 the precipitation rose slightly and cedar growth

rose slightly, but the run-off rose to a high peak, being augmented by the conserved water of 1928.

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SECONDARY GROWTH OF WHITE PINE IN RELATION TO ITS WATER SUPPLY

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There is a general belief in the dependence of tree growth upon climate. The aim of this study is to analyze the relations between the rate of secondary growth in *Pinus strobus* and any climatic factors which can be shown to affect it decisively on sites in northern New England.

Our method of approach has been through large numbers of exact measurements of width of annual rings, tested for their agreement with existing records of rainfall and temperature in the same area. In general, the study has followed the methods initiated by Douglass ('19) and modified for use in New England by Lyon ('36). In the case of *Tsuga canadensis*, there appears to be some positive correlation between its moisture supply and the rate of radial growth. Our purpose is to determine if white pine shows any such relations with its water supply as it is controlled by rainfall and temperature.

REVIEW OF PREVIOUS WORK

There are several generally accepted growth requirements for white pine. Frothingham ('14) pointed out that a porous, well-drained soil is best. Pines often grow in very moist soil but, as Spaulding ('99) found, they are less sensitive to climatic factors in swampy areas and therefore have a more even rate of growth on such sites. On the contrary, white pine at high altitudes and rooted in dry soil is sensitive to variations in atmospheric factors.

Some work has been reported for the height growth of white pine. Baldwin ('31) showed that temperature controls both the start and the rate of primary growth. Schubert ('31) observed that propitious years for growth of "pine" in Germany are characterized by higher rainfall from April to June as well as during July and August of the preceding year. This implies some dependence upon stored foods for the material basis of new growth but secondary growth need show no such dependence.

Previous work of this nature with secondary growth of white pine in northern United States has been done by Brown ('15) in central New York and by Burns ('26) in Vermont. The latter did not take annual measurements but merely failed to detect any relationship between growth and rainfall over an 11-year period. Brown's results are generally interpreted to indicate some control of radial growth by temperature but not by rainfall.

In a study of *Pinus banksiana* in plantations of young trees in northern Vermont, Adams ('28) noticed that "spring rainfalls seem to exert some influence on the thickness of the wood layer," as indicated by a 10-year series of annual measurements.

METHODS AND MATERIALS

The trees used in this study had grown in three groups, each on a well-drained site without unusual features of soil or exposure. The sites used were selected only in the sense that they bore stumps of old pines which had been cut at times known to us through inquiries of the owners. The three sites are located within a radius of 13 miles about the station (Hanover, N. H.) at which the standard observations of weather are made and recorded daily. Its elevation is 603 feet.

The sections of all the trees were taken at stump height, usually above the level of appreciable buttress flares. A group of nine trees were used from a site in Norwich, Vermont. The exposure was northern with a slight, even slope and an altitude of about 750 feet. Ten sections were obtained from Enfield, New Hampshire, the site farthest from the weather records station and with an altitude of about 1,000 feet. This site had no appreciable slope and adjoining areas more or less swampy indicated a relatively high water table but the surface soil was well drained about the trees used for our analyses. The third site at Hartland, Vermont, where eight sections were taken from closely grouped trees, was a slope with northeast exposure at an altitude of 1,115 feet.

Measurements of the rings on the wood sections were made according to the technique described by one of us (Lyon, '36). Each section was measured for width of ring along three average radii, the unit of measurement being .1 mm. The mean of the three widths recorded for each ring was taken as a fair index of rate of secondary growth of the tree, subject to possible but unavoidable variations in width of ring at different levels in the tree.

The age range of the trees was considerable. The Norwich group was the youngest, varying from 42 to 63 years. At the Enfield site the sections averaged 67 rings each. The Hartland trees were all over a hundred years old with a maximum of 121 years. The effect of these differences in ages between the three groups of trees is to limit comparisons between them to a period of about 70 years.

RESULTS

Taking the data as a whole, there was an evident and consistent occurrence of relatively wide or narrow rings for certain years. In other years there was much variation between individual trees of a group and between the mean values calculated for each of the three groups of trees. Since we are not concerned primarily with the cross-identification of individual trees,

but with relationships between growth rates and water supply, the measurements are here presented for the three groups of trees rather than for the individual tree sections. However, cross-identification between the graphs for individual trees was very evident. The variations of single trees with slightly different crowns, root systems and growth responses are practically eliminated by the use of data for groups but differences due to site effects remain.

The mean values of ring widths for each year and for each of the three groups of trees are shown graphically in figure 1. The uppermost curve represents the mean ring widths for all the trees during the years involved at

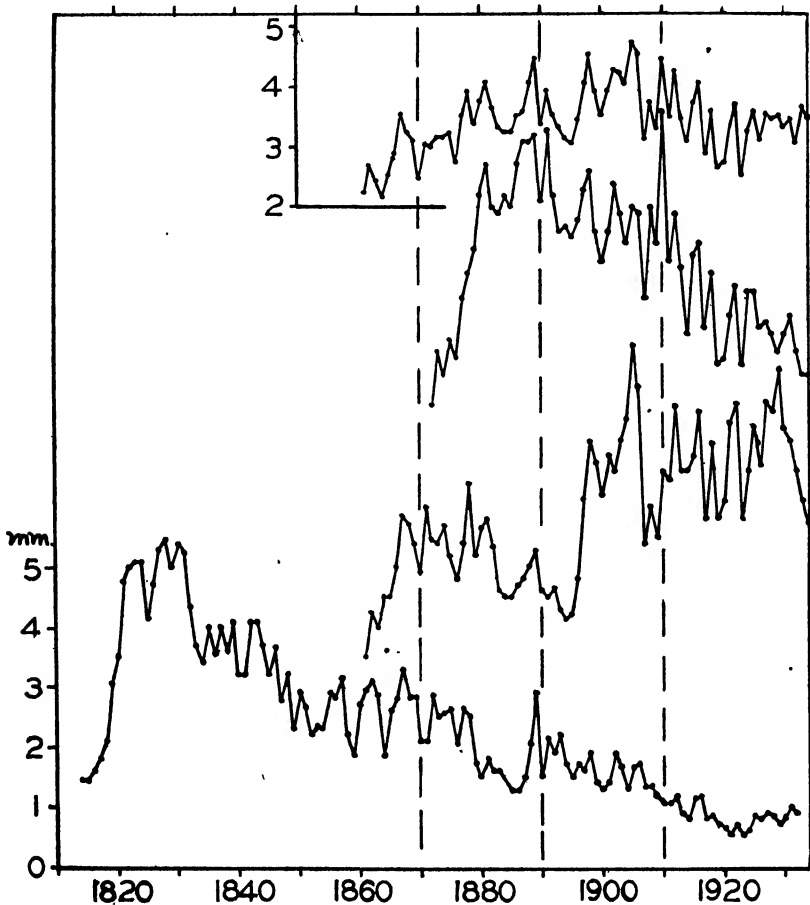


FIG. 1. Comparison of annual secondary growth increments in groups of trees from three sites. Mean ring widths on vertical axis; calendar years on horizontal axis. Reading from bottom to top, the three lower graphs are based on measurements of trees from Hartland, Vt., Enfield, N. H., and Norwich, Vt. The uppermost graph is a composite of the others for the years involved at two or more sites.

two or more sites. It is added here to demonstrate the extent of the agreement in growth rates at the different sites. Inspection will show that this agreement is close for many years characterized by growth rates relatively greater or less than those of years immediately preceding or following. For reasons common to all or at least to two of the tree groups, these years were apparently marked by environmental conditions correspondingly more or less favorable to secondary growth and of more importance than the nutritive conditions at the different sites. Since these years are thereby indicated and since they give the most promise of usefulness in an analysis of direct relations between growth rate and general environmental conditions, they are considered to be "critical years" for the purposes of our analysis. They appear regardless of the absolute values of ring width in the separate graphs for the three sites.

The most clearly defined of these critical years for the area studied have been entered in table I. In general, the years are the same for all the sites.

TABLE I. *Years with maximum or minimum growth rates*

Narrow Rings			Wide Rings		
Norwich, Vt.	Enfield, N.H.	Hartland, Vt.	Norwich, Vt.	Enfield, N.H.	Hartland, Vt.
—	1870	1870	—	1867	1867
1876	1876	1876	1875	—	1875
—	1879	1879	1881	1881	1881
1885	1884-85	1884	1889	1889	1889
1890	—	1890	1891	1892	1891
1895	1895	1895	1898	1898	1898
1900	1900	1900	1902	—	1902
1904	—	1904	1905	1905	1905
1907	1907	—	1910	1910	—
1909	1909	—	1912	1912	1912
1911	1911	1911	1916	1916	1916
1914	1914	1914	1918	1918	1918
1917	1917	1917	1922	1922	1922
1919	1919	—	1927	1927	1927
1923	1923	1923	1931	—	1931

In a few cases, such as 1867 and 1910 for relatively wide rings and 1890 and 1909 for narrow rings, some one of the groups of trees did not register the particularly favorable or unfavorable set of growth factors. It should be noted that the terms "wide" and "narrow" do not refer to absolute values; a wide ring may actually have a smaller width than a narrow ring formed at a different period in the life of the tree.

DISCUSSION

The regular occurrence of these relatively fast or slow growth rates during certain years throughout the area included by the three sites, shows the importance of non-edaphic factors in determining secondary growth rate in

white pine, at least during the critical years. These years are essentially the same as those entered in table I but in view of the lack of perfect agreement among the three lots of trees, it is better to use the composite graph in figure 1 as the final criterion in their selection.

Of the climatic factors recorded by the usual daily observations, only the rainfall of certain periods agrees well with the growth rates in the critical years. Temperature effects seem to be somewhat irregular and will be considered later. The other standard climatic data are not to be related so far as we can judge.

Since there normally appears to be little secondary growth in pine except during May, June and July (Brown, '15), the rainfall of this period could be expected to exert some influence. The amounts recorded for the Hanover station have been entered as curve *B* in figure 2. Because its maxima and minima are obviously not always coincident with the relatively wide and narrow rings of the composite graph for growth (curve *A*), various other periods were also examined. Curves *C* and *D* in figure 2 are entered to show the quantities recorded for two other periods which might be thought to control the water supply of a forest tree in the New England area. Curve *C* represents the rains of the preceding fall plus precipitation during the April-July period. The omission of the intervening months coincides with our experience and belief that frozen ground on sloping sites causes eventual run-off of practically all precipitation during the period of December-March inclusive. The occasional importance of the water supply from the period without snow cover (April-November) in the year preceding the formation of the wood ring was not unexpected in view of the findings for hemlock as reported by one of us (Lyon, '36). The total precipitation of that period was accordingly entered as curve *D*.

In order to make clear the relations between the four curves of figure 2, especially for the critical years in which the effects of the rainfall factor should be evident if it is important, the relations between growth rate and the three periods of rainfall are also given in table II. The presence of a positive correlation between unusual growth rate (wide or narrow ring) and unusual rainfall (high or low respectively) is indicated by a + sign. For most of the 35 years that appear in this analysis, a positive correlation is noted for one or more of the three periods, usually that of the growing season. Notes of other conditions are entered for a few years in which the nature of the growth rate cannot be explained alone by the total rainfall of the three periods here suggested as most important to the pine tree. For example, the high run-off from downpours in July, 1911, accounts for the absence of a positive correlation between slow growth and the rainfall of the May-July period which was actually a drought period in the Hanover area. Over half of the total precipitation for this period fell on July 15, 17, 28 and 29, each day with over an inch of rain.

The conclusion from this comparison between growth rate and water supply for the tree is that rainfall during the season for secondary growth is the dominant element in the complex of climatic factors. When heavy rains occur, the total precipitation must be discounted to the extent that the topography of the site allows appreciable run-off of the water. In about one-third of

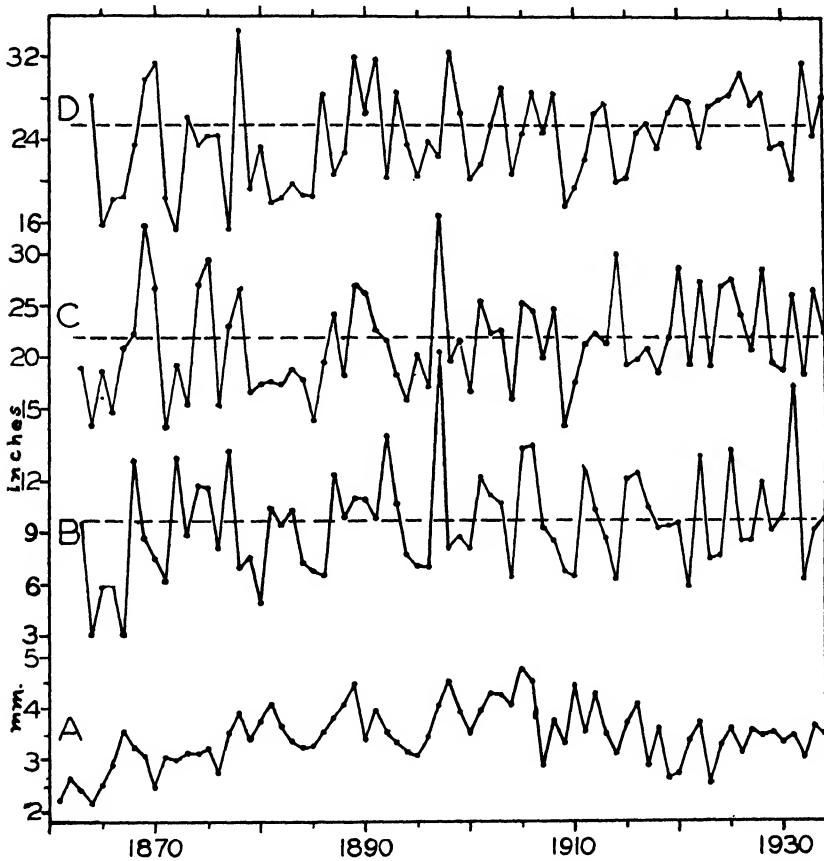


FIG. 2. Annual growth increments of white pine (curve *A*) in relation to total rainfall of certain months. Broken horizontal lines indicate mean rainfall for the periods involved. Curve *B*—rainfall of May-July inclusive. Curve *C*—rainfall of April-July of year in which wood layer is formed plus that of preceding September-November. Curve *D*—total precipitation for April-November plotted one year late. See table 11 for analysis of correlations in critical years.

the critical years, our analysis shows that an important contribution is made to the water content of pine forest soil by the nature of the rains of the preceding fall or by them plus similar rainfall amounts during the preceding summer. Occasionally the rainfall of April becomes significant but this is easier to understand than the few instances of secondary growth apparently

maintained well into August, as in 1867, 1910 and 1918. Unavailable evidence of the exact growing seasons in such years would alone determine this point but two of these three years may not be truly "critical," since the unusual growth rate does not appear at some one of the sites. These and other exceptional years are so few in number, while the general agreement between

TABLE II. *Relations between growth rates and periodic rainfall*
(+ sign indicates positive correlation)

Width of Ring	Year	May-July	Apr.-July plus preced. S-N	Preceding Apr.-Nov.	Additional Notes
Narrow	1864	+	+	-	Wet August
Wide	1867	-	-	-	
Narrow	1870	+	-	-	
Wide	1875	+	+	+	
Narrow	1876	+	+	-	
Wide	1878	-	+	+	
Narrow	1879	-	+	+	
Wide	1881	+	+	-	
Narrow	1884	+	-	+	
Narrow	1885	+	+	+	
Wide	1889	+	+	+	
Narrow	1890	-	-	+	
Wide	1891	-	-	+	
Narrow	1894	+	+	-	
Narrow	1895	+	-	+	
Wide	1898	-	-	+	
Narrow	1900	+	+	+	
Narrow	1904	+	+	+	
Wide	1905	+	+	-	
Narrow	1907	-	+	+	
Narrow	1909	+	+	+	Wet August Dry Apr.; high run-off in July No run-off in April
Wide	1910	-	-	-	
Narrow	1911	-	-	-	
Wide	1912	-	+	-	
Narrow	1914	+	-	+	Dry Apr. & May; run-off in June Wet Aug.; run-off in Sept. Dry Apr.; run-off in May and fall Run-off in April
Wide	1916	+	-	-	
Narrow	1917	-	-	-	
Wide	1918	-	-	-	
Narrow	1919	-	-	-	
Narrow	1920	-	-	-	
Wide	1922	+	+	-	
Narrow	1923	+	+	-	
Wide	1925	+	+	-	
Narrow	1926	+	-	-	
Narrow	1932	+	+	-	
Total + signs		21	19	15	

water supply and growth rate is so consistent, that the data are interpreted by us as sufficient proof of the dominance of the water supply factor.

Our efforts to analyze the effects of air temperatures on growth rates lead us to consider them as less important than the water supply. The daily mean temperatures, computed from the 8 A.M. and 8 P.M. readings, are so obviously of limited value to the problem and so cumbersome to present in statistical

form that we are not presenting the pertinent data in this report. The relations indicated for the years listed in table II can be summarized briefly.

1. Except as temperature affects growth rate through its evaporation effects, low temperatures cause narrow rings and high temperatures tend to produce wide rings. For example, the wide rings of 1898 and 1918 agree with mean temperatures much above average during the normal growing season of May–July, while the narrow rings of 1917 and 1920 (which do not agree well with the rainfall records) may have been affected by the unusually low mean temperatures of their growth periods.

2. The best agreements for direct proportion between growth increment and mean daily temperatures appear during the months of April and May, when over 70 per cent positive correlations were noted.

3. The worst month for positive correlations on the same basis is June, when less than 40 per cent were found. This suggests a negative correlation, perhaps because high temperatures tend toward drought conditions and vice versa during June, in complete agreement with Diller's ('35) conclusion for beech in Indiana.

Since the study of hemlock growth in relation to water supply as reported by one of us (Lyon, '36), was made by the same methods and in part in the same area as this analysis for white pine, it is especially interesting to compare the responses of the two species. They are not wholly identical but the differences are not greater than can be accounted for by the importance of the April and August precipitation for the hemlocks while secondary growth in pine is influenced so greatly by the May–July period only. The greater importance of the temperature factor for pine is another difference which probably works in conjunction with water supply during certain months to cause the occasional appearance of maximum and minimum growth rates in different years for the two species.

The extent of agreement between them is shown by the following data, based on measurements at Hanover alone and with even slight maxima and minima recognized.

Critical years identical for white pine and hemlock:

1867, 1875, 1878, 1879, 1885, 1895, 1898, 1900, 1902, 1903, 1904, 1907, 1910, 1911, 1912, 1914, 1916, 1920, 1922, 1923.

Effects shown a year early in pine:

1864, 1876, 1889, 1890, 1891, 1905, 1917, 1919.

Effects shown a year late in pine:

1870, 1881.

Years indicated by one species only:

by pine—1909, 1925, 1926, 1932.

by hemlock—1872, 1873, 1930.

In view of this good agreement between white pine and hemlock, it should be possible to use the growth rate of either species as an index of

effective water supply in relation to plant growth in given years. Since radial growth in hemlock is governed by a five-month period of precipitation in contrast with the three-month season for white pine, hemlock may be preferable as an indicator for the entire growing season for plants. On the contrary, the better agreement between spring temperatures and the width of ring in pine suggests this species as a better indicator for length of growing season, on the theory that this is determined largely by the time of arrival of the minimum conditions for growth.

SUMMARY

Using the mean width of annual ring as a measure of secondary growth rate, groups of white pine trees grown on three sites in northern New England have been used in an analysis of the relations between their growth rates and existing records of temperature and rainfall in the same area. The total precipitation absorbed by the soil during the season for secondary growth (normally May to July inclusive) is the dominant element in the complex of climatic factors. Residual effects from unusually large or small amounts of rainfall during the snowless period of one year are sometimes reflected in the growth increment of the following year. Temperature effects are confined chiefly to indirect action on the water content of the soil and to a direct effect during April and May. When the temperature factor is important, the width of ring is directly proportional to the temperature. Since the years marked by relatively wider or narrower rings of white pine are essentially the same as those previously reported as producing the same growth effects in hemlock, it is suggested that these two species are about equally responsive to the dominant climatic factor of rainfall.¹

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¹ Confirmation of the essential results of this study has since been obtained by one of us (C. J. L.) from a similar analysis of white pine grown at Conway, N. H. Sections were taken from the butt logs of ten trees in a small woodlot. Comparison of the mean ring widths from the two areas showed that 77 per cent of the narrow and wide rings reported for Hanover appear in the same years at Conway. The airline distance between the two sites is about 65 miles. The measurements for this supplementary work were obtained with the assistance of Mr. R. C. Dickinson, a student at Dartmouth College.

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A STUDY OF POISONOUS DRYMARIA ON SOUTHERN NEW MEXICO RANGES

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Among the harmful plants that grow on clay (adobe) soils on ranges of southern New Mexico, the most poisonous for cattle are dwarf summer annuals of the species *Drymaria holosteoides* Benthani (*D. pachyphylla* Woot. and Standl.). Of more than a dozen species of *Drymaria* occurring in Central America, Mexico, and southwestern United States, members of only the species named are known to be toxic. These plants have been found in southern New Mexico, southwestern Texas, southeastern Arizona, and Mexico.

Because of the great number of deaths of range cattle caused by eating these poisonous plants, a study of them was made by the author in 1934 and 1935, with a view to determining feasible methods of eradication and how livestock losses might be reduced. These investigations were made at the Jornada Experimental Range, U. S. Forest Service, near Las Cruces, N. Mex.

Discovery of these plants as poisonous is recent. In 1922 a cooperative study of them was begun by the New Mexico Agricultural Experiment Station and the Bureau of Plant Industry, U. S. Department of Agriculture. Lantow ('29), of the former institution, demonstrated their extreme toxicity to cattle and sheep in feeding experiments from 1923 to 1927, and found all parts of the plants above ground to be poisonous at all stages of growth. Because of the unpalatability of the plants, forced feeding was necessary. Campbell ('31) showed poisonous drymaria to be a pioneer weed in plant succession on clay soils, and made germination tests of the seeds. Mathews ('33) conducted additional feeding experiments in southwestern Texas in 1932 and determined lethal doses. He reported that the plants caused death in a cow when they were eaten at the low rate of 0.4 per cent of body weight, in a sheep at 0.6 per cent, and in a goat at 0.97 per cent. The toxic principle has not been determined.

PLANT DESCRIPTION

Drymaria holosteoides was described by Benthani (1844) from specimens collected at Cape San Lucas, at the southern tip of Lower California, Mexico, during the voyage of the *Sulphur*, 1836-1842. The New Mexico and Texas plants of the genus *Drymaria* were considered distinct by Wootton and Stand-

¹ Maintained at Tucson, Ariz., by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of Arizona.

ley ('13), who proposed the species name *D. pachyphylla*, which is here regarded as a synonym. The genus *Drymaria* is classed in the tribe Polycarpeae of the Caryophyllaceae.

Poisonous drymaria plants are small, whitish-green or glaucous, tender, glabrous, summer annuals (figs. 1 and 2). They grow only 1 to 3 inches high, and spread out in round clumps from 4 to 5 inches, sometimes to 10 inches, in diameter. Ranchmen identify these plants by an anthocyanin pigment in the immature seeds, which pigment gives the juice of green capsules a purple color. Superficially, the plants resemble the common chickweeds, *Stellaria media*.

The primary root of a drymaria seedling remains as the tap root of the mature plant. Usually the root system is shallow, only 2 to 4 inches in depth, and the tap root below 1 inch has many shorter, fibrous branches. There is no main, erect stem; but from a very short stem at the top of the tap root, from 10 to 20 or more procumbent or partly erect stems spread out in all directions and give the plant a round shape. At a distance of 1 to 2 inches or more, each branch ends in a node, with usually 4 ovate leaves, a cluster of axillary, white flowers one-eighth of an inch broad, and several branches which continue the growth of the plant. About 15 dull black, flattened seeds one twenty-fifth of an inch long are produced in each capsule. Usually a plant 4 inches in diameter with about 250 mature capsules produces as many as 3,750 seeds. The large number of seeds produced by a single plant is obviously an advantage for a desert annual, likewise an obstacle in eradication.

The Lower California plants differ from those of New Mexico in having much narrower, acutish leaves, puberulent pedicels, and slightly smaller seeds.

The microscopic anatomy of roots and stems of poisonous drymarias presents no unusual features but the leaf blade, which is small and succulent, has several xeromorphic characteristics which make the plants somewhat resistant to dry weather and to chemical sprays. It is rather thick (one-fiftieth inch) and compact, when viewed in cross section. On the epidermis of both upper and lower surfaces there is a slight cuticle and a deposit of wax. The palisade mesophyll is composed of two (in places three) distinct layers of compact, elongated cells. The spongy mesophyll, which is as thick as the palisade mesophyll, is also compact. In places the cells of spongy mesophyll are elongated and form two layers of palisade-like cells next to the lower epidermis. The compact leaf cells probably function in water storage as well as in photosynthesis. Stomata are present on both upper and lower surfaces; somewhat more on the upper.

DISTRIBUTION AND HABITAT

Poisonous drymaria has been found in Reeves and Brewster Counties in the Trans-Pecos area of southwestern Texas, in at least nine counties in southern New Mexico, and in Cochise County of southeastern Arizona.



FIG. 1. A plant of the poisonous drymaria.

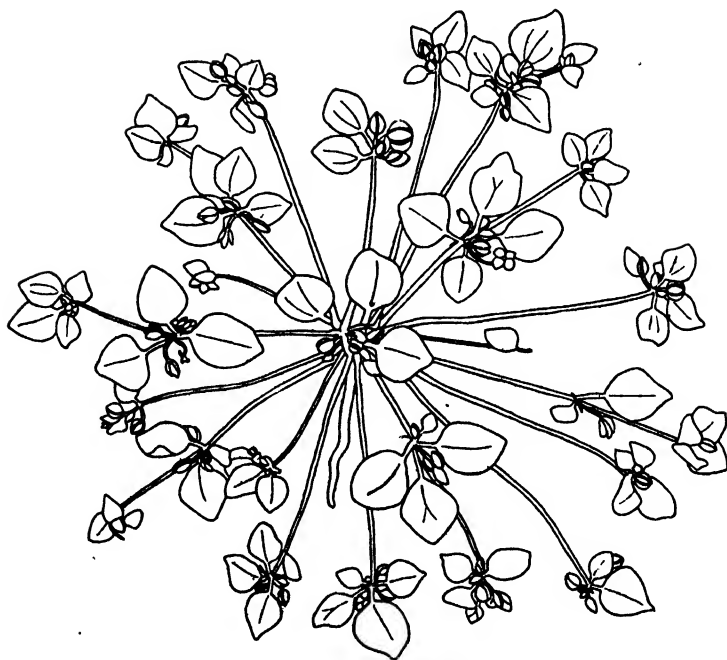


FIG. 2. The branching system of drymaria.

Livestock losses in New Mexico have been principally in: (1) Tularosa basin, which has no outside drainage, in Otero and Lincoln Counties, and (2) Jornada del Muerto plain east of Rio Grande in Dona Ana, Sierra, and Socorro Counties. They have been reported also from Lea, Eddy, Luna, and Hidalgo Counties, New Mexico.

Before it became known and conspicuous as harmful, poisonous drymaria was collected by botanists at only two places in the United States. The first, according to Robinson (Gray, 1897), was by V. Havard in August 1883, at Terlingua Creek, Brewster County, Texas. In New Mexico, E. O. Wooton collected specimens in 1897, 1899, and 1905, all in the same general locality south of White Sands and near Parkers Well, Dona Ana County. Wooton and Standley ('15) mentioned no additional records in their Flora of New Mexico. The absence of specimens in other early collections indicates that these native plants probably have increased in number and range during recent years. On the Jornada Experimental Range, where a Forest Service herbarium was started in 1915, the first record is a collection on an adjacent ranch, made in 1925.

Ranchmen in parts of southern New Mexico state that they found drymaria present and destructive to cattle when they came to their localities 20 or 25 years ago, but the absence of a common name indicates the unimportance of these plants in the past. According to cattlemen, poisonous drymaria is getting more abundant, is spreading to other ranches, and is causing greater losses.

Plants of the species *Drymaria holosteoides* occur in two distinct geographic divisions and in different habitats: (1) in the Chihuahua desert of southwestern Texas, southern New Mexico, southeastern Arizona, Coahuila, and Chihuahua, where they occur on bare adobe flats of plains at elevations of 3,000 to more than 5,000 feet, and (2) along the coasts of Lower California and Sonora, where they grow on subtropical sea beaches, but sometime at higher elevations. These widely separated environments are similar, in that ocean beaches and clay flats are bare, subject to flooding, and contain large quantities of salts. The southern New Mexico portion of the range is in the Lower Sonoran life-zone with semidesert shrub and grass vegetation.

In southern New Mexico poisonous drymaria is confined to areas of clay soils, including clay loams and occurs in shallow gullies and on broad flats where water collects. These soils have a reaction of pH 8 and more. As similar clay soils are common throughout the southwest, it is possible that these plants might spread over a much greater area of several states through dissemination by water, wind, and in mud on the feet of livestock. Ranchmen should be on guard to avoid introduction of seed, and to prevent establishment of these destructive plants in new localities.

LIFE HISTORY

The life history of poisonous drymaria is completed between the beginning of summer rains in July and the first killing frost in the autumn (Nov. 1, average for Jornada range). The annual precipitation at Jornada Experimental Range, a typical area within the range of these plants in southern New Mexico, is only 9.07 inches, of which about half falls during the summer growing season (July, August, and September) and half is fairly evenly distributed over the remaining 9 months. Being annuals and dependent on rainfall, these plants cannot avail themselves of the warm season after the last killing frost in the spring (Apr. 21, average date at Jornada range), because then the soils are dry.



FIG. 3. Seven stages in the development of drymaria seedlings, viewed from above and from the side, natural size.

Commonly, seeds of these plants germinate within a few days after the first heavy summer rain thoroughly wets the surface of clay flats and drainage channels. Rapid germination and growth are advantages in these locations, where soil moisture and humidity soon become unfavorably low. In places, seedlings become established in the cracks of clay soils, where the seeds obviously had been blown by wind. The depth at which germinating seeds are buried is usually one-fourth of an inch or less, but seeds covered as deep as one-half an inch may grow.

A series of drawings of seedlings (fig. 3) is shown to aid in recognition during early stages of growth. Floral buds appear very early, even by the time a plant has only 6 or 8 leaves and is less than half an inch high. Axillary buds develop into long prostrate branches. The plants shed mature seeds

within a month after germination, and continue to flower and produce quantities of seeds until killed by frost or drought. Seeds fall to the ground and remain around the base of the plants until blown by wind into soil cracks, or until carried by water or wind to distant places.

Length of life of poisonous drymaria in southern New Mexico varies from 1 to 5 months, depending on moisture and date of the first killing frost. A single heavy wetting or flooding of the clay flats may furnish enough water for germination, growth, storage of water in the leaves, and maturity of the seeds within a month. Plants continue to germinate and grow as more rain falls, until killing frost. Where the soils are drier, plants are smaller and growth is slower. The fact that these plants are not more widespread undoubtedly is due to the extreme dryness of their habitats during long periods annually.

During wet springs poisonous drymaria appears earlier and livestock losses start earlier than under dry conditions; but in dry summers, such as 1934, plants may be very scarce and short-lived, because of lack of water. The greatest livestock losses occur in late summer and early fall, when the plants are most abundant.

PLACE IN PLANT SUCCESSION

In connection with the possibility of eliminating poisonous drymaria through revegetation, its relation to other plants and animals and its place in plant succession were studied. No native animals were observed to use drymaria either as food or host plant. It is pollinated by insects, mainly bee-flies of the genus *Anthrax*.

Campbell ('31) has described the following four stages (fig. 4) in plant succession on clay soils on the Jornada Experimental Range: (1) pioneer lichen stage, (2) localized ruderal-weed stage, (3) burrograss (*Scleropogon brevifolius*) or first grass stage, and (4) tobosa (*Hilaria mutica*) climax. Poisonous drymaria occurs in the first two.

Commonly, where they occur, drymaria plants are the only ones present as pioneer annuals on bare clay flats—unkindly habitats for most other kinds of plants—where they may attain a density as high as 0.1. Associated with them in the localized ruderal-weed stage are plants that grow in shallow drainage channels, including those of the species *Hoffmanseggia densiflora*, *Chamaesyce albomarginata*, *Wedeliella incarnata*, *Amaranthus graecizans*, and *Cheirinia elata*.

As drymaria is a pioneer on clay soils, it would seem that it might be slowly eliminated during the next stage in succession, the burrograss or first grass stage; but no evidences of crowding and shading by other plants were observed. Burrograss is a low perennial which, in mats, may vary in density from 0.1 to 0.35, and which may spread by means of stolons and sets. Although seeds are abundant and become lodged in cracks on bare clay, seedlings of burrograss are not common. On a quadrat at the edge of a burrograss mat

on the Jornada range, this grass has advanced about 130 cm. onto bare clay in a 19-year period, which rate may not be typical, because that period includes years of drought and heavy grazing. Burrograss has some natural protection from overgrazing, in that it is palatable only a few weeks in the summer, after which the long-awned florets protect it from grazing animals. Because of the slow rate of succession on clay flats in this semiarid climate, natural revegetation will be too slow for immediate eradication of drymaria, but it may prove to be an inexpensive solution to reducing the number of these plants on badly deteriorated lands.



FIG. 4. Three stages of plant succession in the revegetation of an adobe flat: in the foreground a ruderal-weed stage of poisonous drymaria; farther out, burrograss; and in the background, tobosa grass.

Unfortunately, with the deterioration of grass cover on large areas, due to overgrazing, and the consequent accelerated erosion and deposition of clay, the bare flats apparently have increased in size, and the pioneer, unpalatable drymaria is becoming more abundant.

GERMINATION TESTS

Information on viability and longevity of seeds is needed in studying eradication of drymaria, whose only means of survival from one year to the next is in the form of seeds and whose eradication seems to hinge on prevention of seed production. Campbell ('31) tested drymaria seeds at Jornada Experi-

mental Range, and the author made additional germination tests in Petri dishes and folded blotters at ordinary room temperatures in a dark room.

The average germination of 17 tests of 100 seeds each (produced in 1933 and tested in 1934) was 30.6 per cent. Most of the seeds germinated within a week. There were delayed germination and dormancy also, which are important factors in the continuation of the plants in following years.

Germination is rather low just after the seeds mature. The results of 11 tests of 1934 seeds immediately after maturity (2.8%) agreed with Campbell's test of October 1929, which gave 3 per cent.

A test of 100 selected seeds collected January 17, 1934, from dead plants hoed in August 1933 gave 42-per cent germination. Thus, hoeing of mature plants may not necessarily prevent reproduction by seeds.

Seeds from herbarium sheets were tested to obtain information on longevity, but none from the New Mexico collections of 1897, 1899, and 1905 germinated. One test of 1925 seeds, almost 9 years old, gave 23 per cent, and another test gave no germination. Seeds of 1929 and 1931 collections had higher germination percentages. As seeds retain their viability several years, follow-up eradication seems necessary for a few years.

Because run-off floods the clay flats and is an important factor in seed dissemination, experiments were made to determine what effect the soaking of seeds in water would have on germination. Seeds in lots of 100 were soaked 7, 14, 21, and 28 days; check samples were kept dry. The results showed that soaking of seeds 7 days increased germination, but caused decay of seeds that did not germinate; and that soaking for longer periods caused decay of all seeds. Thus, under natural conditions, flooding for short periods may increase germination and at the same time may increase decay of seeds that do not germinate at once.

ERADICATION STUDIES

The principal means of preventing losses from poisonous drymaria and other poisonous range weeds are (1) proper range management, including light stocking and conservative grazing, to give the assurance of sufficient good forage; (2) judicious handling of livestock, such as herding the animals away from infested areas, and fencing such areas; and (3) actual eradication through such methods as grubbing or hoeing, cultivation, burning, and spraying with chemicals. Eradication of range weeds is similar to the controlling of farm weeds, except that the lower values involved do not justify much expense. Control of annuals, such as drymaria, concerns principally the prevention of seed production. The alternative of cure by medical treatment of poisoned animals is not likely to succeed, because cattle soon die after eating drymaria.

Fencing on the Jornada range was confined to two areas, one of 90 acres and the other of 4,500, fenced in 1930. But fencing proved to be expensive,

and did not solve the problem, because these plants became common on other parts of the range.

Eradication by hoeing was tried in 1933, 1934, and 1935. As these weeds are delicate, shallow-rooted annuals which can be killed simply by scraping with one's shoe, it is not necessary to cut off the plants more than half an inch below the ground surface. A sharp, broad-bladed hoe is the best tool. If seeds are present, the hoed plants should be put into sacks and destroyed.

Several ranchmen have tried eradication by cultivation methods, using drags and other kinds of harrows. It is possible that making soils more open through harrowing might favor the growth of drymaria the next year. Where these plants are scattered, mixed with other plants, or occur in gullies or other areas that are not level, drags or harrows cannot be used.

The use of kerosene and gasoline burners was successful. The burners tested included one made for destroying weeds and also a "pear" burner used by ranchmen in removing spines from prickly-pear cacti in their preparation for forage. Burning was slightly faster than hoeing; but the flame seemed to blow the seeds already on the ground into clay cracks instead of destroying them.

Of five chemicals tried in spraying tests with a hand-spray tank, 10 per cent sulphuric acid proved to be satisfactory. This acid, which is superior to most chemicals under conditions of low humidity, caused drymaria leaves to begin to wilt and turn yellow and brown within a few minutes.

As an indirect way of combating poisonous drymaria, as well as aiding nature and increasing forage production, revegetation of clay flats by transplanting and seeding of six native grasses was tried. But the experiments of 1934 were failures, because of drought; and attempts to hasten plant succession by applying sand on clay flats were also unsuccessful. Artificial revegetation, even if successful, would be too expensive and too slow a measure.

Of the several methods tested, hoeing is to be preferred in most cases, because it is least expensive, it allows convenient and time-saving travel on horseback, and it enables better use of labor or helps to reduce unemployment by providing more temporary work. Dragging or harrowing, if shown by further tests to be successful, might prove to be the quickest and cheapest way of ridding large patches on level areas.

RECOMMENDATIONS FOR CONTROL

Measures for control of poisonous drymaria on southern New Mexico ranges may be classed as permanent and temporary. Permanent measures involve revegetation, which is slow in semiarid regions. Before natural revegetation can occur, overgrazing must be stopped. Even if natural conditions can be restored through protection from grazing or by conservative use, there probably will always be a few small bare areas of clay where poisonous drymaria will grow.

During natural restoration of the ranges, there are several temporary methods that may be effective in reducing livestock losses from drymaria. The first is reduction in number of cattle, in order to assure more forage per animal. Experience has shown that where plenty of forage is available, cattle losses from unpalatable poisonous weeds, such as drymaria, are light. Other methods that may be applied would differ on each range according to such factors as losses, abundance and distribution of drymaria and clay flats, and cost of eradication.

Action should be taken as soon as drymaria seedlings (fig. 3) first appear after summer rains begin. If there are livestock losses, all cattle should be removed immediately from suspected areas, otherwise the losses might mount overnight.

Where drymaria is restricted to small areas, fencing of these patches may be the best solution. But the possibility that these weeds may spread from a fenced area to other parts of a range should be considered. On ranges where there are areas of soils other than clay, those parts or areas overrun with drymaria may be isolated by fencing. Herding or riding to keep cattle away from infested areas is also suggested.

On ranges where poisonous drymaria is widely distributed, annual hoeing, or hoeing combined with dragging or harrowing of large patches on level areas, is probably the best solution. Eradication work should begin as soon as possible after these plants start growth in July or earlier, in order to prevent or reduce seed production. Mature plants bearing seeds should be put into sacks and destroyed. In wet years it may be necessary to hoe more than once, because seedlings may continue to appear after rains during the summer.

The possibility of eradicating drymaria permanently is not encouraging, because of the difficulty of locating all rapidly growing, scattered plants before some have borne seeds. Although hoeing will have to be done each year, it is possible that these poisonous weeds can be greatly reduced after a few years of thorough eradication before seeds form.

If the cost of application of these methods is greater than the value of the forage and profits from the range lands involved or greater than the value of the cattle killed, the only other immediate solution seems to be deferred grazing or removal of cattle from infested ranges during the wet summer months while drymaria is growing. Deferred grazing will result in a loss of forage, because the principal grasses of clay flats (burrograss and tobosa) are palatable only in summer. However, the grasses will benefit thereby.

SUMMARY

The characteristics and life cycle of poisonous drymaria (*Drymaria holosteoides* Bentham or *D. pachyphylla* Woot. and Standl.), which occurs on ranges of southern New Mexico, were studied with a view to control and

mitigation of livestock losses. These harmful annuals have increased during recent years as the result of overgrazing.

To meet these problems, reduction of cattle in order to assure adequate forage is suggested. Also, eradication on small areas through hoeing, and in large level areas through dragging or harrowing seems cheapest and most satisfactory.

Permanent control seems to be through natural revegetation, although this process takes time.

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CHANGES IN THE INVERTEBRATE COMMUNITY OF A LAGOON AFTER DISAPPEARANCE OF THE EEL GRASS

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INTRODUCTION AND DESCRIPTION OF AREA

In 1923 while the eel grass, *Zostera marina*, was flourishing in suitable areas around Woods Hole, W. C. Allee completed a study of the animal communities of the region, and described in some detail the one characteristic of the eel grass areas. In 1931 practically all the Woods Hole eel grass was killed by a mycetozoan parasite, and today it is still very scarce. Interest in the possible changes in the animal community led to a new survey made in early September, 1936.

The area which Allee found to show the eel grass community best is a shallow lagoon in the Northwest Gutter, a channel running between Naushon and Uncatena Islands. In 1923 the portion of this lagoon which was always covered by at least 30 centimeters of water was filled with a dense matting of eel grass. In the summer of 1936 the lagoon floor was a vast extent of muck without any plant covering. The eel grass was gone except for one or more small patches about one square meter in area, and the many dead rhizomes still in the mud were the only evidence of its former abundance.

THE INVERTEBRATE COMMUNITY BEFORE AND AFTER

In his most detailed analysis Allee subdivides the area into two communities, but in his general quantitative faunal list he treats it as a single unit, and for this general comparison I shall do the same. Formerly, the animals of the area were of four types: those living upon the plants, those living among them, those upon the surface of the mud, and those burrowing among the roots in the mud. Characteristic forms of the first type were the anthozoan, *Sagartia luciae*, the bryozoan, *Bugula turrita*, and the gastropods, *Bittium alternatum* and *Littorina littorea*. Swimming forms belonged to the second type; the annelid, *Podarke obscura*, was frequently abundant, and the small shrimp, *Virbius zostericola*, and the scallop, *Pecten irradians*, were numerous. The third group, those living just on the surface of the mud, was composed of crustacea and molluscs. The annelid, *Scoloplos fragilis*,² was the most abun-

¹ Contribution No. 134 of the Woods Hole Oceanographic Institution.

² This form was first identified in part as *Scoloplos acutus*: see Allee, '34, and Dawson, '31, for discussion of this point.

dant and characteristic of the group burrowing in the mud. Now, only the last two of these major types are to be found. My observations and collections, summarized in the second column of table I, indicate that, of the characteristic animals of the first two types, *Littorina littorea* and certain crustacea moved to the surface of the mud when the eel grass went out, and the others disappeared completely. No such significant change occurred in the bottom forms. Table I allows a comparison of the occurrence of the important members of the population before and after the disappearance of the *Zostera*. A decline of about one-third of the number of species after the extermination of the grass is evident; the total decreased from 55 to 36 and no species new to the area since 1923 were noted. The short period of collecting for the 1936 study does not seem an important factor in this.

Allee's faunal list was compiled from the collecting reports of over 50 crews of students in the course in Invertebrate Zoology at the Marine Biological Laboratory. Each crew reported a species as either present or absent in their collections, and it is reasonable to assume that the number of crews reporting a species was roughly proportional to the abundance of the species, although also in part proportional to its conspicuousness.

A comparison of the total population of the area before and after the epidemic would be of interest in regard to possible changes in the total number of individuals and in their total mass, but the 1923 data are not suitable for this.

COMPARISON WITH CONDITIONS ON THE ENGLISH CHANNEL

The results of this study on the Massachusetts coast should be compared with the observations of Marcel Prenant regarding the effects of the disappearance of *Zostera marina* in the Morbihan, a bay on the southern coast of Brittany. The epidemic left only a few scattered plants of *Z. marina* there, and *Z. nana* and *Chorda filum* have only partially replaced it. There the effects of the loss have been greater than those near Woods Hole. The disappearance of the mat of vegetation permitted increased current scouring and hence changes in the composition of the sediments. Epiphytic forms diminished in number for lack of support, but they are present still where *Z. marina* is now found. Decrease in the proportion of fine particles in the sediments has been accompanied by important changes in the fauna of the bottom.

QUANTITATIVE STUDY OF THE BURROWING ANIMALS

The disappearance of the eel grass around Woods Hole may have had both direct and indirect effects. Directly, it has brought a loss of feeding grounds, shelter, and support, and in these aspects it has not been replaced. Indirectly, the disappearance of the plant may have caused changes in the water circulation in the lagoon, changes in the amount of dissolved oxygen, in temperature, and in pH. The relative importance of the physico-chemical changes com-

TABLE I. Showing the relative abundance of characteristic species in the N. W. Gutter lagoon before and after the disappearance of the eel grass³

I. Animals formerly growing on the plants	Occurrence		III. Mud-surface forms (continued)	Occurrence	
	Before	After		Before	After
Coelenterata: <i>Sagartia luciae</i>	* 4		<i>Nassa obsoleta</i>	***	**
Bryozoa: <i>Bugula turrata</i>	***		<i>Nassa trivittata</i>	**	**
Arthropoda: <i>Idothea baltica</i>	*		<i>Modiolus demissus</i>	***	
Mollusca: <i>Bittium alternatum</i>	**		<i>Mytilus edulis</i>	**	
<i>Lacuna vincia</i>	**		<i>Ostrea virginica</i>	*	*
<i>Littorina</i> sp.	***	**	Total number of characteristic mud surface species	16	12
<i>Mitrella lunata</i>	*		IV. Burrowing forms		
Total number of characteristic epiphytic species	7	1	Nemertea: <i>Cerebratulus lacteus</i>	*	*
II. Animals formerly swimming among the plants			<i>Micrura leidyi</i>	***	
Annelida: <i>Podarke obscura</i>	*		Echinodermata: <i>Leptosynapta inhaerens</i>	***	*
Arthropoda: <i>Crago septemspinosa</i>	*	*	<i>Thyone briareus</i>	***	**
<i>Gammarus</i> sp.	**	**	Annelida: <i>Amphitrite ornata</i>	**	*
<i>Palaemonetes vulgaris</i>	**	**	<i>Arabella opalina</i>	**	**
<i>Virbius zostericola</i>	**		<i>Cistenides gouldi</i>	**	**
Mollusca: <i>Pecten irradians</i>	**		<i>Clymenella torquata</i>	**	***
Total number of characteristic swimming species	6	3	<i>Diopatra cuprea</i>	*	
III. Animals living on the surface of the mud			<i>Glycera</i> sp.	***	*
Coelenterata: <i>Hydractinia echinata</i> ⁵	**	**	<i>Lumbrineris tenuis</i>	*	***
Arthropoda: <i>Carcinides maenas</i>	**		<i>Maldane urceolata</i>	*	*
<i>Libinia dubia</i>	*		<i>Nereis virens</i>	***	
<i>Libinia emarginata</i>	*	*	<i>Scaloplos fragilis</i>	***	***
<i>Pagurus longicarpus</i>	***		<i>Spio setosa</i>	*	***
<i>Pagurus pollicaris</i>	*	*	<i>Phascolosoma gouldi</i>	*	*
<i>Neopanope texana sayi</i>	**	*	Arthropoda: <i>Pinnixia chaetoptera</i>	*	*
<i>Limulus polyphemus</i>	**	*	Mollusca: <i>Cumingia tellinoides</i>	**	
Mollusca: <i>Crepidula convexa</i>	**	**	<i>Ensis directus</i>	*	*
<i>Crepidula fornicata</i>	*	*	<i>Macra lateralis</i>	*	*
<i>Crepidula plana</i>	**	*	<i>Mya arenaria</i>	***	*
			<i>Solemya velum</i>	**	
			<i>Tellina tenera</i>	**	**
			<i>Venus mercenaria</i>	**	**
			Chordata: <i>Dolichoglossus kowalevskyi</i>	*	*
			Total number of characteristic burrowing species	25	20
			Grand total of characteristic species	55	36

³ Allee ('23a) lists 138 species found in the eel grass areas from 1915 to 1921. Of these, 18 species were never found in the N. W. Gutter and 64 species were so rarely present there as to be found only during one or two years, or else were so scarce in number as to be found by only one or two collecting parties a year; these very rare species have been considered unimportant in the population as a whole and have therefore been omitted from this list for the sake of clarity.

⁴ * Occasional: Before—found in less than 33 per cent of Allee's collections. After—forming less than 2 per cent of the 1936 population.

** Common: Before—in 33 per cent to 50 per cent of Allee's collections. After—forming 2 per cent to 5 per cent of total population.

*** Abundant: Before—in over 50 per cent of Allee's collections. After—forming 5 per cent or more of the total population.

⁵ Since the hermit crabs, on whose shells this hydroid lives, are to be found on the surface of the mud, this seems the best place to classify *Hydractinia*.

pared to the biotic changes remains to be investigated, but Prenant's study suggests that the direct effects are probably the major ones at Woods Hole as well as in Brittany.

The change brought the burrowing forms into prominence, and a census of these was made. At low tide, samples were collected at ten different points in the lagoon, then under 15 to 45 cms. of water. A unit area of 0.1 sq. meter was inclosed by a sheet iron frame 20 cms. wide and 50 cms. long. All the sediment within the frame to a depth of 30 to 40 cms. was shoveled out and placed in buckets until it could be sieved. All specimens retained by the $3\frac{1}{2}$ mm. mesh were saved, identified, and counted. About 275 individuals of 23 species formed the population of one square meter. Table II lists the species found, and their abundance.

TABLE II. *Abundance of 23 species at various stations*

Species	Total number animals	No. of stations where found	Stations									
			1	2	3	4+5	6	7	8	9	10	
<i>Scoloplos fragilis</i>	86	10	1	5	11	19	2	15	17	4	12	
<i>Clymenella torquata</i>	52	8	3	16	5	24	1	0	0	1	2	
<i>Lumbrineris tenuis</i>	41	8	1	8	6	11	7	0	2	6	0	
<i>Spio setosa</i>	23	8	0	7	9	3	1	1	1	1	0	
<i>Tellina tenera</i>	16	6	3	0	1	1	4	0	0	3	4	
<i>Cistenides gouldi</i>	14	7	0	1	6	3	0	1	0	2	1	
<i>Nassa trivittata</i>	10	5	6	1	1	0	1	0	0	1	0	
<i>Macra lateralis</i>	8	5	0	1	1	0	2	2	2	0	0	
<i>Venus mercenaria</i>	5	3	1	0	0	0	3	0	0	1	0	
<i>Arabella opalina</i>	4	3	0	2	0	0	1	0	1	0	0	
<i>Pinnixia chaetoptera</i>	5	2	0	0	0	3	0	0	0	2	0	
<i>Maldane urceolata</i>	3	2	0	2	0	1	0	0	0	0	0	
<i>Cumingia tellinoides</i>	2	2	0	0	0	0	0	0	0	1	1	
<i>Amphitrite ornata</i>	2	2	0	0	0	1	0	0	0	1	0	
<i>Glycera americana</i>	2	2	0	1	1	0	0	0	0	0	0	
<i>Mya arenaria</i>	2	2	0	0	1	0	1	0	0	0	0	
<i>Dolichoglossus kowalevskyi</i>	2	1	2	0	0	0	0	0	0	0	0	
<i>Cerebratulus lacteus</i>	1	1	0	0	0	1	0	0	0	0	0	
<i>Ensis directus</i>	1	1	0	0	0	1	0	0	0	0	0	
<i>Lyonsia hyalina</i>	1	1	0	0	0	0	0	0	0	1	0	
<i>Haminea solitaria</i>	1	1	0	0	0	0	0	0	0	1	0	
<i>Phascolosoma gouldi</i>	1	1	1	0	0	0	0	0	0	0	0	
<i>Unicola irrorata</i>	1	1	0	0	0	1	0	0	0	0	0	
Total	273											

I am indebted to Dr. A. C. Redfield for advice on this study, to Dr. W. C. Allee for suggestions and for approval of my interpretation of the condition of the eel grass community as he studied it, and to Mr. G. M. Gray for several of the identifications.

SUMMARY

A comparison has been made between the animal communities of a typical eel grass area before and after the almost complete extermination of the

plants by a mycetozoan parasite. The data came from Allee's papers on the animal communities of Woods Hole and from my observations and quantitative survey of the burrowing animals of the area. As might be expected, practically all the animals once found living on or among the eel grass disappeared with it, and although the total number of burrowing species fell slightly, they now constitute a much larger proportion of the population than formerly. The decrease in complexity of environmental conditions due to the disappearance of the vegetation has been accompanied by a decrease in the number of characteristic species from 55 to 36, a loss of one third, and no new species have been noted.

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TUBER PRODUCTION OF THE COLORADO WILD POTATO AS INFLUENCED BY CERTAIN ENVIRONMENTAL FACTORS

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The Colorado wild potato, *Solanum jamesii*, lends itself well to studies dealing with a comparison of the physiological responses obtained when plants are grown under different conditions of altitude, nature and air content of the soil, and temperature.

The range of this species is from the mountains of the extreme southwestern portion of Colorado to New Mexico and Arizona. Fitch¹ who described the plant as found in its native habitat near Durango, Colorado, gives its height as about 2 decimeters and refers to its slender, non-spreading habit. When cultivated in a garden plot where sufficient moisture is available, it grows to somewhat greater height and is more bushy in appearance. Figures 1-5 illustrate the vegetative, floral, and fruiting characters of this species. The leaves are pinnately-compound with 7-9 leaflets, lanceolate to ovate-oblong in shape. The cymose inflorescence bears few to many white, star-shaped flowers. The tubers which are produced on rhizomes may extend to a considerable distance from the main root system. They range in length from 5 to 25 mm., with an average weight of less than one gram and have been described by Fitch as "perfect little early Ohios." The first tubers employed, which were secured from Snowflake, Arizona, were light brown in color and gave no indication of the purple coloration which appeared in some of those grown in Colorado at an altitude of 5,500 feet or higher.

The sections of this paper dealing with the number and weight of offspring as influenced by age of mother tubers and by the soil used, and the effect of freezing on sprouting were contributed by the junior author; the remainder is by the senior author.

YIELDS AT DIFFERENT ALTITUDES

Wild potatoes planted in three different localities in the vicinity of Boulder, Colorado, varied considerably not only in yield but also in color. Tubers of one group were planted in the University greenhouse in sandy loam in March and were harvested in September; those of a second group were grown at the head of Boulder Canyon at Nederland, which has an altitude of 8,000 feet. The area where the potatoes were planted was freshly plowed sod, and parts of the plot were rather sandy due to washings from a near-by road.

¹ Fitch, C. L. 1921. The Colorado wild potato. *Potato Mag.* 3: 26-28.



FIGS. 1-5.

- FIG. 1. Two wild potatoes from a garden plot with plenty of moisture.
FIG. 2. A greenhouse plant in flower.
FIG. 3. A portion of the root system of the wild potato with tubers.
FIG. 4. Flower much enlarged.
FIG. 5. Fruit of the wild potato, 11 mm. in diameter.

Tubers of the third group were grown in mellow loam in a garden plot close to the foot hills in Boulder, altitude 5,500 feet.

The tabulated results (table I) indicate that more than twice as many tubers per hill were produced at an altitude of 8,000 feet as were produced in

TABLE I. *Yield of wild potatoes at different altitudes in Colorado*

	Greenhouse	Alt. of 8000 ft.	Alt. of 5500 ft.
Total no. of hills.....	167	183	84
Total no. tubers harvested.....	2,791	7,101	5,140
Av. no. per hill.....	16.6	33.3	62.2
Av. wt. per tuber (in gm.).....	.69	.78	.93
Av. wt. per hill (in gm.).....	11.5	26.1	56.8
Percentage of purple tubers....	—	25.7	17.5

the University greenhouse. Those grown in the garden plot in Boulder produced more than three and a half times as many per hill as did those in the greenhouse. The average weight of those grown at 5,500 feet was 35 per cent greater than those grown in the greenhouse, while those at 8,000 feet were 13 per cent heavier.

Seed balls were produced in abundance out-of-doors at an altitude of 5,500 feet; a few were formed at 8,000 feet, but there were none on the plants grown in the greenhouse. These fruits are about 12 mm. in diameter, greenish in color with some purple around the calyx end of the berry (fig. 5).

All the mother tubers planted were russet tan in color. However, 17 per cent of the offspring which were grown in the open at 5,500 feet had purple coloration while 25.7 per cent of those grown at 8,000 feet were likewise colored. Microscopic examination showed that most of the color was present in the outer layer of the cortex. In some, only the outermost layer was colored; in others, the outer 2 or 3 layers were purplish, while in a few cases there seemed to be purple streaks even in the interior.

COMPARISON IN NUMBER AND WEIGHT OF OFFSPRING PRODUCED BY BROWN AND PURPLE MOTHER TUBERS

Tubers from a garden plot at an altitude of 5,500 feet were planted the latter part of May at Nederland, Colorado (altitude 8,000 feet), and a comparison made of offspring from 50 hills each of purple and brown mothers. Brown offspring are commonly produced in greater abundance by both brown and purple mothers than are the purple ones. However, the proportion of purple offspring was greatly increased when plants were grown at this altitude, for in this experiment they composed 35 per cent of the entire crop. They were larger also than the brown ones, their average weight being 53 per cent greater. The purple mothers produced one-third more tubers per hill, and showed 19 per cent increase in average weight per tuber. The purple mothers developed over twice as many purple offspring per hill as did the

brown mothers, as well as a greater number of browns per hill. The brown offspring from purple mothers were 16 per cent heavier than the browns from brown mothers.

DORMANCY OF TUBERS AS INFLUENCED BY COLOR AND AGE OF MOTHER

When tubers of the same age were kept at room temperature, a high percentage of the purple ones sprouted within two weeks after they were dug while practically all of the brown ones remained dormant.

Fourteen-month-old brown tubers which had been stored in a cool basement were used for a comparative study of the difference in age of the mother on time of sprouting and on the production of young tubers. Two groups of 36 pots each were utilized in this experiment; the first contained 3 brown tubers to each pot; the second, an equal number of purple. After sprouting-records were taken, two plants only were left in each pot so that there would be sufficient room for development of new tubers. At the conclusion of the experiment, it was found that the young purple tubers gave the higher percentage sprouting. The older brown ones produced a slightly greater number of offspring per hill but with less average weight. The average weight of offspring from the younger tubers was 25 per cent greater than that from tubers produced by the older mothers.

In order to determine the approximate age at which the greatest number of brown potatoes would sprout, tubers harvested in October and afterwards stored in a cool basement, were planted in the greenhouse monthly from November to April inclusive. At the end of a nine-month period when the experiment was concluded, only 16 per cent of those placed in pots in November and December had sprouted. A greater number of those planted in January and April sent up shoots than did those of the other groups. There was some delay, however, even in these groups so that the highest percentage of sprouting, which was 83 per cent in the April planting, was not secured until late July.

Results from the above greenhouse experiment agree with those obtained in field studies in which tubers planted 6 or more months after harvesting gave a greater number producing shoots than did those which had been in storage in a cool basement for but three months.

The junior author found that when brown potatoes which had been stored in a cool basement for two months were kept at 9° C. for one month, dormancy was broken and 100 per cent sprouting occurred.

SPROUTING OF MOTHER TUBERS AND PRODUCTION OF OFFSPRING AS INFLUENCED BY SOIL

Tubers were planted in three kinds of soil: a mixture of one-third loam and two-thirds sand, pure garden loam, a mixture of three-fourths loam with one-fourth fertilizer of well-decayed stable manure. Twenty-four pots of

each kind of soil with three tubers to each pot were arranged to allow uniform light, heat, and moisture conditions. A record was kept of the number of tubers of each age sprouting during a ten-week period.

When complete records of the sprouting had been taken, one tuber was removed from each pot, leaving but two. These were allowed to mature, and the number and weight of young tubers in each pot recorded. Weighings were made twenty-four hours after digging.

Pure loam proved to be the best soil in which to sprout tubers; sandy loam was next, followed closely by the loam containing fertilizer (table II).

TABLE II. *Sprouting of mother tubers and production of offspring as influenced by soil*

	Pure loam	Sandy loam	Fertilized loam
No. of pots.....	24	24	24
Percentage sprouting in 9-week period..	86.1	79.1	76.4
Av. no. offspring per mother tuber.....	11.1	8.4	15.7
Av. wt. offspring per mother tuber (gm.)	13.6	10.8	23.8
Av. wt. per tuber (gm.).....	1.2	1.3	1.5

EFFECT OF FREEZING ON THE SPROUTING OF WILD POTATO TUBERS

Two series of experiments were carried out to determine whether (1) tubers could be frozen solid for a short period of time and live, and also (2) whether they could retain their viability if held at approximately 0° C. for a considerable period of time. In the first experiment, four hundred tubers were placed in large test tubes, which were corked and immersed in a mixture of ice and salt kept at a temperature of —15° C. Every hour for 8 consecutive hours, 50 tubers were removed and planted in garden soil in the greenhouse. The percentage sprouting after a four-week period ranged from 44 per cent of those frozen for one hour, to 62 per cent of those frozen for 8 hours. Seventy-two per cent of the untreated tubers sprouted within four weeks.

In the second experiment, the tubers were kept at a temperature of 0° C. for periods varying from 3 to 12 days. The temperature was kept fairly constant by means of an ice-salt mixture. Every three days, 50 tubers were removed from the containers and planted in the greenhouse. Forty-eight to 64 per cent sprouted after they had been frozen several days. This would indicate that some injury had occurred but not enough to kill all the tubers. The length of time they had been held in a frozen condition did not make any marked difference in the percentage forming sprouts. From the results of these two experiments, it is evident that freezing of the tubers lessens the percentage sprouting but does not totally inhibit their growth.

INFLUENCE OF WELL-AERATED SOIL ON TUBER DEVELOPMENT

A well-marked tendency toward better tuber production in areas where the soil was well aerated was noted in each of the different habitats where the

wild potatoes were grown. The plot of ground in the mountains was formerly occupied by an aspen thicket which had been plowed just previously to the time of planting. A few old roots remained in the soil, and an unusually large number of tubers developed in hills where these were present. Tubers were also produced in greater abundance around pieces of old, partly rotted pieces of wood or even around stakes used for marking row number. In some cases, stolons had penetrated well rotted pieces of wood, and tubers had formed within the wood.

In the garden plot in Boulder, more tubers were present where long tap roots of mallow had loosened the soil, allowing an increase in the air content.

Potatoes in the greenhouse were grown in one-cubic-foot plots which had been partitioned off with boards, and the compartments filled with soil of uniform character. When the tubers were dug, it was apparent that not only were more produced in the corner plots than in the interior ones, but that the greater number was near the cracks where boards were joined. In some of the side plots where cracks allowed the entrance of more air, tubers were present in greater numbers than in plots with less opportunity for air circulation.

Actual counts and weights of the tubers produced showed that in the outside plots there was 29 per cent increase in average number of tubers per hill and 35 per cent increase in average weight per hill. Thus both field and greenhouse observations support the conclusion that well-aerated soil is conducive to the best production of wild potato tubers.

SUMMARY

The Colorado wild potato is suitable for use in experiments dealing with the effect of certain environmental factors upon growth because of the small size of the tuber and the ability of the plant to grow readily either in the greenhouse or outside in a garden plot.

A comparison of the yield of greenhouse-grown tubers with those from garden plots at different altitudes showed that in the latter habitats an increased weight of individual tubers as well as increased number per hill was evident.

Although the original tubers obtained from Arizona were all russet tan in color, 17 per cent of the young tubers grown in the open in Colorado at an altitude of 5500 feet were purple, while 25 per cent of those grown at 8000 feet were likewise colored. In most cases the color was confined to the outer layer of the cortex. Purple mother tubers produced not only a greater number of tubers per hill than did the brown mothers, but the individual weight was also greater.

Brown potatoes have a longer period of dormancy than do the purple ones. However, if the former are kept at a low temperature for a time, dormancy will be broken.

Young purple mother tubers gave a higher percentage sprouting with a greater average weight per tuber than did the older brown ones. Pure loam proved to be the best soil in which to sprout tubers; sandy loam was next, followed by loam containing fertilizer. The greatest number of tubers with the greatest weight per hill was produced in fertilized loam.

Wild potato tubers are produced in greater abundance in areas where the soil is well aerated.

Freezing tubers at 0° C. lowered the percentage sprouting but did not kill all the tubers. 48–68 per cent of those which were kept in a frozen condition for several days put forth sprouts. The length of time the tubers were held at a freezing temperature did not make any marked difference in the percentage which remained viable.

REVIEWS

THE PHYSIOLOGY OF FRESHWATER FISHES¹

This book on the physiology of freshwater fishes is a welcome contribution to the subject. The volume brings together into a convenient and well coordinated handbook the widely scattered literature, much of which is not readily available. The material also constitutes an important background for many ecological problems relating to freshwater fishes.

The author interprets his subject in a broad sense and includes both the gross anatomy and the histological structure of the various organs where such information will contribute to a better understanding of their physiology. These anatomical features are well illustrated in the figures, along with physiological apparatus and records obtained in experiments.

The nine chapters deal with the physiology of the skin, and the sense organs, as well as with that of the nervous, respiratory, blood, digestive and muscular systems, and finally with that of reproduction and embryonic development. Limited space permits only a brief consideration of some of the salient points.

Under the function of the skin, the author discusses the slimy covering, the pigment cells, the color changes, and the scales, including the winter rings on the latter which are an index of age. The discussion of the senses includes temperature, taste, hearing, sight and equilibrium responses. In respiration three general classes of fish are recognized with reference to oxygen requirements, namely high, medium and low; several examples are given for each of these groups. The effect of the carbon dioxide content of the water is also referred to.

The chemical composition of the blood is given, as well as the number of red and white corpuscles found in several species of fish; three different types of sera are indicated. Consideration is given to the amount and kinds of food consumed at different seasons of the year, to the rate of digestion and to vitamin requirements. One section is devoted to internal secretions. Each chapter closes with a list of references to original literature that deals with the particular subject under consideration.

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¹ **Wunder, Wilhelm.** 1936. *Physiologie der Süsswasserfische Mitteleuropas*. Bd. II B. *Handbuch der Binnenfischerei Mitteleuropas*. 340 pp., 213 figs. 9 pls. *E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart*. Price (Ausland) Mk. 36.75.

THE VEGETATION OF HAITI¹

This geobotanical study is confined largely to the eastern portion of the island occupied by the Dominican Republic. This area is only half cultivated and offers great contrasts in elevation and in climatic conditions. The physiography and geology are sketched and a rainfall map shows annual precipitation varying from 500 to 3500 mm. resulting in a wide and complex range of vegetation types extending from scrub and savanna to mesophytic and rain forest. A map shows the distribution of these communities.

The different plant communities are described in considerable detail and the various successional series traced. Some idea of the complexity both of the vegetation and of the author's terminology may be had from the revision of the terminology of climax communities which is presented. In it a con-climax, a euclimax and pseudoclimaxes are distinguished and defined. The pseudoclimaxes include preclimax, postclimax, anteclimax, subclimax, meta-climax, paraclimax, transclimax, peniclimax and proclimax.

Following the terminology three principal conclimaxes are distinguished. That of the xerophytic complex includes the euclimax (central climax) hyperxerophytic forest of Cactaceae, the subxerophytic forest of *Phyllostylon-Acacia* and the thorn thickets (*Macchia spinosa*) of *Brya-Pictetia-Pithecolobium*. Associated with these are communities of *Prosopis juliflora*, of a short grass prairie of *Bouteloua-Sporobolus* and a palm barren of *Sabal-Coccothrinax*.

The second and most important conclimax of the rudomesophytic forest includes the euclimax of the mesophytic forest, an association of *Catalpa-Swietenia*, a rain forest of *Spondias-Oreodoxa* on neutral soil and one of *Sloanea-Ormosia* on acid soil. Here are included postseral and subseral associations of the forest on the north side of the island, the chief of which is a community of *Pinus occidentalis* with several variations.

The conclimax of the montane-alpine forest includes the euclimax forest of *Garrya-Wcinmannia* and the high mountain forest of *Pinus occidentalis*.

All of these present many variations and subordinate communities, and include a multitude of species (more than 2000) which are listed. The whole constitutes an important contribution to our knowledge of the vegetation of the West Indies.

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¹ Ciferri, R. 1936. Studio geobotanico dell' isola Hispaniola (Antille) [with English summary]. *Atti Dell' Istituto. Bot. Univ. Pavia Sc. 4. 8:* 1-336.

SWISS GEOBOTANY¹

Many ecologists will be interested in the three works which have recently appeared as *Beiträge zur geobotanischen Landesaufnahme der Schweiz*, especially since only one other number has appeared in this series in the past four years. The first is a comprehensive study of the ecology of field weeds in northeastern Switzerland in which the author attempts to determine the extent to which the occurrence, range and vigor of approximately two hundred species depend upon the system of land use and upon climatic and soil conditions. The study is based upon detailed estimates of frequency, dominance (cover) and abundance, correlated with systems of crop rotation, and the determinations of pH, clay and calcium contents of the various soils. Data are also given for the weed seed content of various soils, and its germination capacity.

The other publications are of interest primarily to plant sociologists. Dr. Moor's contribution is a typical publication of the Montpellier school. He treats in detail five associations of the alliance *Nanocyperion flavescentis* Koch. The alliance is withdrawn from Koch's order *Nanocypereto-Polygonetalia* and placed in Braun-Blanquet's *Isoëtetalia*. The alliance *Isoëtion* in the latter order receives a limited treatment.

Dr. Schmid has studied the relict forests of *Pinus sylvestris* in the Alps as a part of his investigation of the vegetational belts of central and southern Europe. Ten associations, all dominated by Scotch pine, are described in the approved Zurich-Montpellier manner, and their occurrence and composition are correlated with present climatic, geologic, topographic, edaphic and anthropic factors, as well as with postglacial floristic and vegetational history.

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THE LIVING WORLD¹

Many ecologists owe their early inspiration to "nature study" as taught in elementary schools, and teachers of biology in high school commonly draw heavily upon the naturalist and the ecologist for the subject matter with which to intrigue the developing mind. Dr. Williams is a naturalist with long and varied field and teaching experience and it is natural that his text book should contain many ecological facts of use to the high school and elementary school

¹ **Buchli, Math.** 1936. *Oekologie der Ackerunkräuter der Nordostschweiz. Beit. Geobot. Landes. Schweiz* 19: 1-354. Fr. 9.80.

Moor, Max. 1936. *Zur Soziologie der Isoëtetalia. Beit. Geobot. Landes. Schweiz* 20: 1-148. Fr. 6.50.

Schmid, Emil. 1936. *Die Reliktföhrenwälder der Alpen. Beit. Geobot. Landes. Schweiz* 21: 1-190. Fr. 9.50.

¹ **Williams, S. H.** 1937. *The Living World. Macmillan.* \$3.60.

teacher who desires to stimulate the normal interest of the child in the living world about him.

The book covers a wide field including both plants and animals, although the emphasis is more upon the animals. It would be impossible to treat each phase thoroughly and at the same time treat the whole field extensively in a book designed for practical use by teachers. The organization is partially ecological and partially taxonomic. Practical aids to field study are included. The illustrations are numerous. The text is well written and interesting.

Some of the interpretations of biological phenomena are somewhat uncritical and a few of the examples used in discussing various theories are questionable. The book should be of use to the teacher of pre-college biology, however, who should approach the subject more from the viewpoint of the naturalist instead of simplifying the average college course in elementary biology.

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ECOLOGY IN THE STUDY OF MEN ¹

Professor Bews has attempted to coordinate, between two moderately spaced book covers, all and sundry of the overlapping social, geographic, and psychological sciences as a holistic science of man and his environments. Such an undertaking, though predestined by its very nature to be elementary if not superficial, is a step in the direction of synthesizing the present welter of predominantly analytic studies of man.

The philosophic observations contained in the introductory sections constitute in the reviewer's opinion the book's most significant contribution. "Ecology," says Professor Bews, "represents not so much a branch of biological science as a certain attitude of mind with regard to life." This attitude is described as consisting of the holistic viewpoint and the synthetic as well as analytic method. General J. C. Smuts, former Premier of the Union of South Africa, says in his introduction, "The progress of scientific knowledge and technology is continuously revolutionizing our human environment. . . . Ecology will supply scientific clues which in the end may lead us on to the right track."

Unfortunately the book omits all mention of this rapidly changing environment and rarely so much as refers to machine civilization or to the interrelations of men's changing environments and their world-views and ethical codes. It is in fact an encyclopedic compilation of the more elementary systematized knowledge of man-environment interactions interspersed with merely stated problems and unanswered questions, and an occasional original but partial synthesis.

¹ Bews, J. W. 1935. *Human Ecology*. 312 pp. *Oxford University Press, London*. \$5.00.

As an example of the type of synthesis found in the book, Professor Bews assumes that the low cultural level of the African pigmies is a product of interactions between tropical rain forest environment and hereditary biotic factors. He correlates this culture with an irregular, highly varied diet consisting of foods such as fungi, roots, ants, larvae, caterpillars, mammals, etc., and this diet is superficially correlated with a powerful, highly plastic digestive system.

From this sort of a beginning two developments are possible in the pursuit of ecology, neither of which is followed by Professor Bews in any instance. A scientist can go on to show something like the ecology of a race, that is, produce a regional study—in this instance, let us say, correlations between calcium deficiency of rain forest environment with small body size, high survival value of small stature in the jungle, the correlations of small stature with blow guns and poisoned weapons, and the correlations of poison with witchcraft and tribal organization. Or, a scientist can investigate the ecology of individual habits, traits, and organs. Let us say in this case, the great plasticity of digestion in pigmies, as a part of the above organism-environment system, could have been contrasted with its high specialization in the Eskimos and the Tibetans and the chemical, cultural, biotic, and other factors of their heredities and environments.

While the enormous scope of this medium sized book inevitably precludes the realization of any of its objectives, it nevertheless serves as an introduction to the field and an initiation to the ecological attitude of mind. As such it can be of value in elementary courses.

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NOTES AND COMMENT

FLORA AND FAUNA OF BRACKISH WATER

For many years man has been occupied in the study of living things found in salt or in fresh water but it is only recently that he has turned his attention to similar studies of organisms found in brackish water. One reason for this late interest in brackish water is man's recent investigations in ecology, especially in those communities where adverse conditions restrict the number of species to a minimum. Such communities provide opportunities of studying plant and animal interrelationships which may otherwise be obscured in more normal and consequently more complex situations. Another reason is in connection with problems related to the movements of fish such as the Atlantic and Pacific salmon which pass through brackish water on their way to or from the sea. A more recent interest in brackish-water life from the evolutionary standpoint is shown in Pearse's¹ investigations regarding possible migration routes from sea to land.

In the fall of 1931 the writer began a study of a brackish-water community under the direction of Dr. C. McLean Fraser, Department of Zoology, and Dr. A. H. Hutchinson, Department of Botany, University of British Columbia. Continuation of the investigation to the present time was made possible by Dr. W. A. Clemens of the Pacific Biological Station, Nanaimo, and by Mr. P. A. O. Sankey, Secretary of the Stanley Park Fly Fishing Association, Vancouver. The assistance given and the facilities provided are much appreciated.

The opportunity of studying organisms found in waters of low salinity was made possible in Lost Lagoon at the entrance to Stanley Park, Vancouver, B. C. This small body of water, formerly a part of Coal Harbour, is now cut off from the sea by an embankment constructed in 1916 (fig. 1). Its water contains much less salt than that of the neighbouring harbour due to a small inflow of fresh water from the city water supply by way of an inlet stream at one end. However, despite the continuous flow of fresh water into the lagoon, the amount of salt in the water has remained appreciable as a result of a constant seepage of sea water through the embankment and of leakage past the valve in the overflow pipe at high tide. A series of water samples taken from the upper 12 inch layer of water in the main part of the lagoon show that the salinity, measured as chlorinity, has also varied according to the season (fig. 2) being high in the summer due to evaporation and low precipitation, and low in the winter due to increased rain-fall. This condition is evident for the year 1934-35 but is disturbed on two occasions during the following year (May and December) by deliberate additions of sea water.

In the course of this brackish-water study several interesting facts have come to light. It has been found, for example, that the animals and plants existing in such environments can be separated into three main groups according to their origin; a marine group, a fresh-water group, and a brackish-water group. The first group contains organisms which normally live in the sea but can tolerate rapid changes in salinity and can even exist under fresh-water conditions. The second contains fresh-water species which are able to withstand the presence of salt water in small amounts. The third group consists of animals and plants which are usually found in waters of low salinity, occasionally in fresh water and only rarely in sea water. They may be classified as brackish-water species. Organisms of this last group show a most discontinuous distribution, possibly as a result of the comparative scarcity of suitable environments.

¹ Pearse, A. S. 1936. The migrations of animals from sea to land. *Duke Univ. Press. Durham, N. Carolina.*

Although the conditions produced by varying amounts of salt water in the lagoon have been somewhat rigorous so far as the animals and plants are concerned, many species have survived and several species have even flourished. An annotated list of the predominant forms is presented.

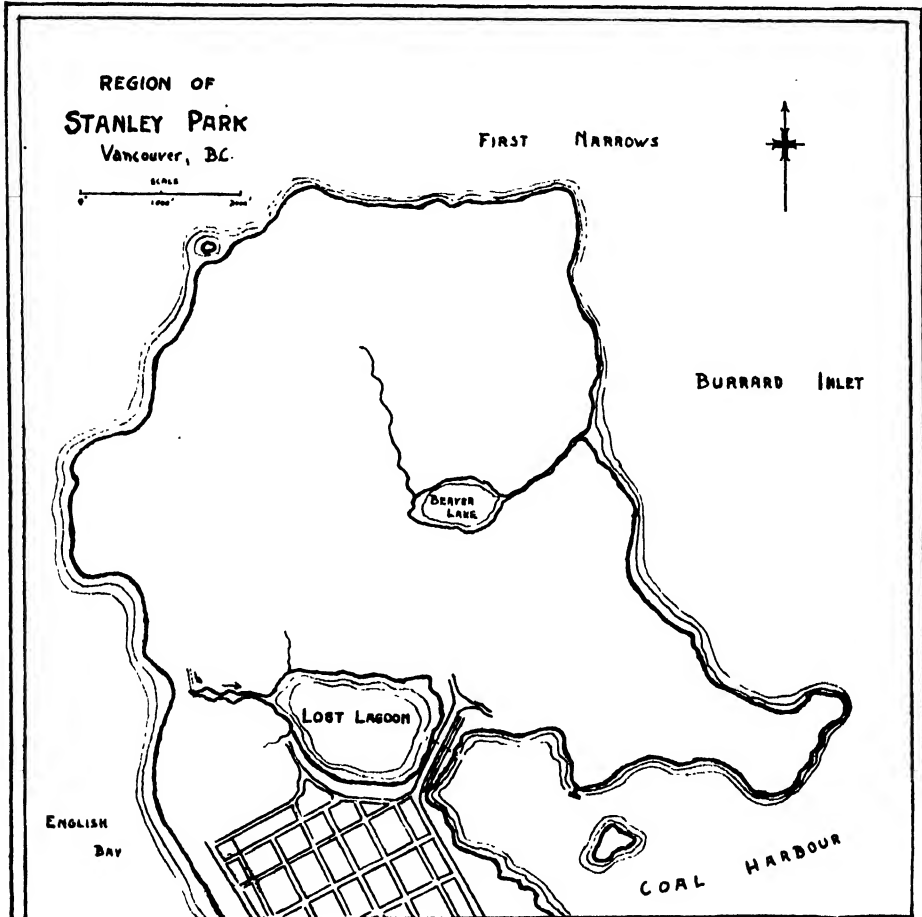


FIG. 1. Map showing Lost Lagoon and its relation to other bodies of water.

CYANOPHYCEAE

Lyngbya bergei Smith

This fresh-water species occurred during the summer of 1932 as an extensive surface "bloom" which eventually disintegrated with no observed ill effects upon the fish.

Anabaenopsis elenkini V. V. Miller

This fresh-water alga flourished particularly during the summer of 1933 and in August it occurred in such large numbers that its sudden death was responsible for the death of many fish, possibly as a result of asphyxia or of the production of protein poi-

sons.² It was present again in 1934 but only in relatively small numbers, and reappeared in June of the following year but in an almost insignificant amount as indicated in figure 3. If figures 2 and 3 be compared it will be seen that a large inflow of salt water occurred at this time which undoubtedly restricted the growth of this fresh-water alga.

DIATOMACEAE

The following typical fresh-water diatoms occurred at various times in the plankton but usually in small numbers: *Tabellaria fenestrata* Kütz., *Cyclotella meneghiniana* Kütz., *Asterionella formosa* Hass., *Melosira varians* Ag.

The first population peak shown in figure 2 was due to the growth of *Tabellaria*; the second peak in November and December was caused by *Cyclotella* which persisted through

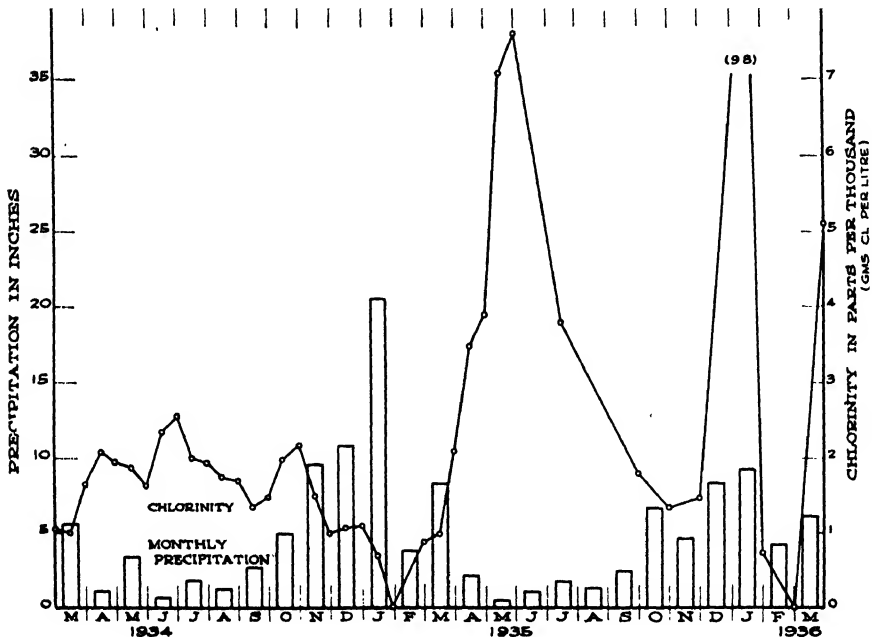


FIG. 2. Graph illustrating the changes in salinity (chlorinity) of surface water in Lost Lagoon, Vancouver, B. C., from March 1934 to March 1936, and its relation to monthly precipitation during the same period.

the winter and rose to a minor peak in February and March of 1935. Diatoms did not occur in appreciable numbers during the rest of the observed period probably on account of the high salinities which prevailed.

CHLOROPHYCEAE

Spirogyra sp.

This filamentous fresh-water alga was found to be abundant during the early part of the summer of 1935 but it soon died out at the time of the increase in the salt content of the water.

² Prescott, G. W. 1933. Some effects of the blue-green alga *Aphanizomenon flos-aqua* on lake fish. *Collecting Net* 7 (4).

HIGHER PLANTS

Ruppia maritima L.

This plant is found only in brackish water but is world-wide in its distribution. In the lagoon its rank growth in the summers of 1934-36 was such as to impede the progress of row-boats.

Fresh-water plants such as the water-lily (*Nuphar polysepala*) and the milfoil (*Myriophyllum verticillatum* L.) which were introduced from the neighbouring Beaver lake, exist in the fresher parts of the inlet stream but did not survive in the lagoon. However, marsh forms such as the cat-tail (*Typha latifolia* L.) and the brackish-water reed (*Scirpus robustus* Pursh.) flourish along the water's edge in all parts.

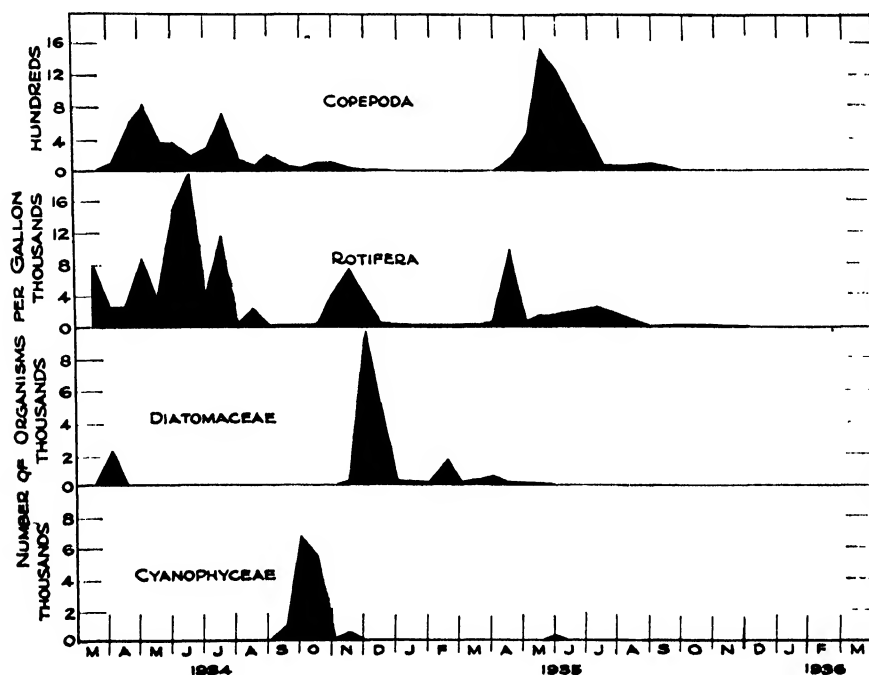


FIG. 3. Showing the fluctuations in numbers and seasonal distribution of four groups of plankton organisms collected from the surface water of Lost Lagoon, Vancouver, B. C., during the period from March 1934 to March 1936.

PROTOZOA

Ceratium hirundinella Müller*Peridinium inconspicuum*

These two fresh-water dinoflagellates were found in the plankton on several occasions during spring and fall but only in small numbers.

ROTIFERA

At times, particularly following the decay of dead algae, rotifers were abundant in the lagoon giving the water a milky appearance. The following species were commonly found: *Keratella cochlearis* var. *tecta* Gosse, *Keratella cruciformis*, *Notholca striata*

Ehrenberg, *Brachionus urceus* Linné, *Brachionus plicatilis* Mobius, *Trichocera* sp. and *Synchaeta* sp. These are fresh-water forms except *N. striata* and *B. plicatilis* which are characteristic of brackish water.

The series of rotifer population peaks shown in figure 3 during the spring and early summer of 1934 were due to the presence of *Keratella cruciformis* which increased in numbers during November and again in April of 1935 when it was associated with *Brachionus plicatilis*.

ANNELIDA

The worms were represented by two marine species, identified by Mrs. C. Berkeley, Pacific Biological Station, Nanaimo.

Nereis japonica Izuka

This sea-worm which is very common in Japan, is very closely allied to *Nereis diversicolor* O. F. Müller which is widely distributed in brackish waters of Europe. The occurrence of *N. japonica* in Lost Lagoon, where it was found in large numbers during August 1933, provided the first known record for the Pacific Coast.

Polydora sp. probably *socialis* Schwarza

Larvae of this worm were found in the plankton during May 1935. It is possible that they were carried into the lagoon by sea water which was allowed to enter at that time.

COPEPODA

The copepods found in the plankton were represented by four species, each with a rather unusual distribution.

Nitocra typica Boeck

This copepod which was identified by Dr. R. E. Coker, University of North Carolina, appears to be of European origin. According to Gurney³ it is found in brackish water of high salinity but only occasionally between tide-marks. It has been recorded from the Atlantic Coast of North America⁴ but there seem to be no previous records for the Pacific Coast.

Mesochra rapiens (Schmeil)

This species also appears to be identical with the European species according to Dr. Coker. In the Old World it is commonly found in fresh and brackish water but has not been recorded from sea water.³ Previous to its recognition in Lost Lagoon it had not been found in North America.

Ergasilus turgidus Fraser

This is a parasitic species the females of which were found originally on the gills of the marine viviparous perch *Cymatogaster aggregatus*. In the lagoon the host is the common stickleback, *Gasterosteus aculeatus* L. which is heavily parasitized. The free-living males, identified by Dr. C. B. Wilson, were found in the plankton in large numbers particularly during May, June and July of 1934 as shown in figure 3.

³ Gurney, R. 1932. British fresh-water copepoda. Vol. II. Ray Society, London.

⁴ Wilson, C. B. 1932. The copepods of the Woods Hole region, Massachusetts. U. S. Nat. Mus. Bull. 158.

Eurytemora affinis (Pope)

This copepod which was abundant during May 1935 coincident with the increase of salinity, is widely distributed in fresh and brackish water of Europe and Asia and is occasionally found in the sea.⁵ It has been found on only a few occasions in North America.⁶

ISOPODA

Two species of Isopods are found in the lagoon, one from salt water and one from fresh water.

Exosphaeroma oregonensis (Dana)

This is a common isopod found in the inter-tidal zone along the Pacific Coast. Although it is essentially a marine species it has also been recorded from fresh water.⁷ In Lost Lagoon it is found in considerable numbers under bits of wood and stones along the shore and is taken by the trout as part of their diet.

Asellus tomalensis Harford

This form is of fresh-water origin being common in neighbouring lakes and ponds.⁸ It occurs in the lagoon in small numbers and in the least saline portions.

AMPHIPODA

Two marine species of amphipods exist in the lagoon.

Gammarus confervicolus (Stimpson)

This is a brackish-water form commonly found in streams entering the sea and occasionally in fresh water.⁹ In Lost Lagoon it flourishes in large numbers.

Corophium spinicorne Stimpson

This amphipod is a tube-dwelling species usually found in the sea at the mouths of rivers. Only a few of these Crustacea were found in the lagoon.

MYSIDACEAE

Neomysis mercedis Holmes

This mysid has been recorded from only a few localities on the Pacific Coast.¹⁰ A few specimens were collected from the lagoon on one occasion only, July 1932.

INSECTA

Odonata

Damsel flies are represented by nymphs of *Enallagma* sp., probably *cyathigerum* Charpentier, which were present in considerable numbers.

⁵ Gurney, R. 1931. British fresh-water copepoda. Vol. I. *Ray Society, London*.

⁶ Esterly, C. O. 1925. The free-swimming copepods of San Francisco Bay. *Univ. Cal. Pub. Zool.* 26 (5).

⁷ Richardson, Harriet. 1905. Monograph on the isopods of North America. *Bull. U. S. Nat. Mus.* No. 54.

⁸ Fee, A. R. 1926. Isopods of Departure Bay and vicinity with descriptions of near species, variations and colour notes. *Contr. Can. Biol. Fish. N. S.* 3 (2): 13-46.

⁹ Saunders, L. G. 1933. Fresh-water amphipods of Vancouver Island. *Contr. Can. Biol. Fish.* 8 (19): Series A, No. 38.

¹⁰ Tattersall, W. M. 1933. Euphausiacea and Mysidacea from Western Canada. *Contr. Can. Biol. Fish. N. S.* 8 (15): Series A, No. 38.

Hemiptera

Water-boatmen, *Callicorixa praecustus*, are sufficiently common as to be often eaten by trout.

Diptera

Midge fly larvae (Chironomidae) were found in quite large numbers in the bottom mud at all times.

MOLLUSCA

Fresh-water snails are represented by two species, *Physa* sp. and *Lymnaea* sp. both being introduced from a neighbouring lake.

PISCES

The fishes in the lagoon consist of four species, three of which have their origin in the sea.

Gasterosteus aculeatus L.

The common stickleback, which is found in both salt and fresh water, forms a large part of the fish population and is an important article in the diet of the trout. At certain seasons, particularly near the end of summer, the sticklebacks are heavily parasitized by the copepod *Ergasilus* mentioned above.

Cottus asper Richardson

The prickly bullhead is found in many bodies of fresh water connected with the sea and, like the stickleback, probably entered the lagoon by way of Coal Harbour before the completion of the embankment. There appear to be no records from salt water. Both young and adults are present in the lagoon in considerable numbers.

Platichthys stellatus (Pallas)

The starry flounder is a marine flat-fish which occasionally wanders into fresh water. In Lost Lagoon only a few individuals were seen in 1932 and 1933 and these apparently were not thriving. None were seen after 1934.

Salmo clarkii Richardson

The cutthroat trout was first introduced in the spring of 1929 when 100 adults and 200 yearlings were liberated in the lagoon. More fish of various sizes were placed in the lagoon at different times during the following years and many were removed by angling during the year 1932. The fish caught were in good condition. Examination of their stomach contents showed that they had been feeding upon sticklebacks, damselfly nymphs and water boatmen.

Salmo gairdneri kamloops (Jordan)

Fry of the Kamloops trout were introduced at various times but it is thought that none survived since none were caught.

From the above list it is apparent that only certain types of organisms have been able to tolerate the conditions obtaining in the lagoon. Pearse¹ has pointed out that in the change from marine to brackish- or fresh-water habitats many factors are involved, including changes in equilibrium between body fluids and external medium, changes in the supporting power of the external medium, changes in food types, increased difficulty in respiration, and increased temperature range. Thus, according to him, marine organisms which are able to adjust themselves to these changes have done so by developing new ranges of toleration or new resistances. That all the animals of marine origin found in the lagoon have not been equally successful in this respect is evident by the fact

that some of them, such as the mysids and the flounders, have finally disappeared while others, such as the amphipod *Corophium* and the isopod *Exosphaeroma*, have not only persisted but, in the case of the latter, appear to be increasing in numbers. However, it is unlikely that these and other marine forms would survive a complete change to fresh-water conditions since they are still dependent upon the presence of a certain amount of salt as shown by their preference for areas near the points of entry of traces of sea water.

The fresh-water organisms in the lagoon also flourish according to their adaptability. The most successful animals are the gastropods and the insects which appear to be least dependent upon the nature of their external environment since they are well distributed throughout the lagoon. Other less tolerant forms, such as some of the higher plants and the isopod *Asellus* failed to become established in the lagoon proper, but still persist in small numbers in the fresher parts of the inlet stream. The lower fresh-water plants, which are planktonic, are found distributed throughout the lagoon but they tend to disappear during times of high salinity. Their re-establishment is probably dependent upon a new supply being carried into the lagoon from the fresher portions of the inlet stream.

The remaining plants and animals such as the ditch grass *Ruppia*, the copepod *Eurytemora*, the amphipod *Gammarus conferviculus*, and the fishes *Gasterosteus aculeatus* and *Cottus asper* which possess a wide salinity toleration (euryhaline) are the dominant organisms within the lagoon and appear to be well established. They are found in all parts of the lagoon proper and some of them, particularly the fishes, are found in the freshest water of the inlet stream.

Further studies of brackish-water communities may provide records which will show that many of the euryhaline species formerly considered to be rare are in reality common and widespread. Future investigations of other lagoons, sea-shore ponds and river estuaries will undoubtedly contribute much in this respect. In this way a more complete knowledge may be gained of their distribution which, at present, is so strikingly discontinuous. How these organisms became so peculiarly distributed presents a problem of which there appears to be no adequate explanation at present.

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DIRECT MICROSCOPIC EVIDENCE OF AN AUTOCHTHONOUS BACTERIAL FLORA IN GREAT SALT LAKE

Popular literature still records that no life can exist in the concentrated brine of Great Salt Lake, an extremely saline body of water in northern Utah covering an area of 1,120 square miles. There is no extensive body of water which surpasses it in density. At the present time it is saturated with sodium chloride, sodium sulfate and probably calcium carbonate. Water samples collected in December 1935 contained 336.23 grams of salt per liter. As late as 1889 David Starr Jordan¹ stated that only the brine shrimp could live in such an environment. More recent literature summarized by Pack,² who himself recovered two ciliates from the lake, reports the presence of nine algae, two protozoa, one crustacean, and two fly larvae. Flowers³ describes the vegetation of Great Salt Lake but does not mention bacteria. Daines⁴ who was the first to report the

¹ Jordan, D. S. 1889. Report of exploration of Colorado and Utah during the summer 1889. *Bull. U. S. Fish. Com.* 9: 31-68.

² Pack, D. A. 1919. Two ciliates of Great Salt Lake. *Biol. Bull.* 36: 273-284.

³ Flowers, S. 1934. Vegetation of the Great Salt Lake region. *Bot. Gaz.* 95: 353-418.

⁴ Daines, L. L. 1917. On the flora of Great Salt Lake. *Amer. Nat.* 51: 499-506.

presence of bacteria in the lake, isolated five species and demonstrated as many as 625 bacteria per ml. of lake water on nutrient agar containing 2.5 per cent NaCl. However, the recovery of bacteria from the water under these conditions fails to prove that they are species indigenous to the lake and not merely passive contaminants, particularly in view of the fact that Frederick,⁵ working in the same laboratory, reported that lake water is not germicidal for freshwater bacteria. Daines recognized this and he states that the most conclusive evidence that native bacteria are active in the lake is the occurrence of putrefaction and decay.

In view of our present day information on the occurrence and activity of bacteria in strong brines, reviewed by Benecke⁶ and by Hof,⁷ one may expect to find a varied microflora in Great Salt Lake. Since the conventional plate count procedures yield knowledge which is both uncritical and incomplete, it was deemed desirable to apply the direct microscopic technique to a study of the lake microflora. Henrici⁸ has shown that a film of microorganisms which can be stained and observed microscopically develops on glass slides submerged in freshwater lakes. He concludes that while the procedure is not offered as a substitute for pure culture studies it "does offer a short cut towards an ecologic survey of water bacteria." Later he described several new species of bacteria by this procedure. ZoBell and Allen⁹ have applied the method to the study of marine bacteria.

EXPERIMENTAL

The controlled laboratory experiments are discussed first because they aid in the interpretation of the field results. Sterile quart jars were filled with raw lake water all of which was previously mixed in a five gallon bottle. Several clean sterile slides (3×1 inches) were inserted in each jar and the jars were covered with Petri dish tops. The jars were held at different temperatures ranging from 4° to 25° C., approximately the seasonal temperature range of water in the lake. After varying periods of submergence slides were removed, washed free of salt in running water, stained and examined microscopically.

It should be emphasized that throughout these experiments the bacteria were not fixed to the slides by heat or otherwise. The criterion of periphytic bacteria is their ability to attach themselves so tenaciously to the slide that they are not dislodged by washing and the subsequent staining procedures. Incidentally, even the prolonged submergence of glass slides in solutions containing dead bacteria does not result in their adherence. Therefore it is believed that true periphytes must be actively growing in order to attach themselves to the slide. While stalked bacteria similar to those described by Henrici have not been observed in Great Salt Lake, most of those which occur on the

⁵ Frederick, E. 1924. On the bacterial flora of Great Salt Lake and the viability of other microorganisms in Great Salt Lake water. *Master's Thesis, Univ. of Utah*, 65 pp.

⁶ Benecke, W. 1933. Bakteriologie des Meeres. *Abderhalden's Handb. der Biol. Arbeitsm., Abt. IX*, 404: 717-872.

⁷ Hof, T. 1935. Investigations concerning bacterial life in strong brines. *Recul Trav. Bot. Neerl.* 32: 92-173.

⁸ Henrici, A. T. 1933. Studies on freshwater bacteria. I. A direct microscopic technique. *Jour. Bact.* 25: 277-286.

———. 1935. Stalked bacteria, a new order of Schizomycetes. *Jour. Bact.* 29: 3-4.

⁹ ZoBell, C. E. and E. C. Allen. 1933. Attachment of marine bacteria to submerged slides. *Proc. Soc. Exper. Biol. Med.* 30: 1409-1411.

———. 1935. Significance of marine bacteria in the fouling of submerged surfaces. *Jour. Bact.* 29: 239-251.

submerged slides have a definite holdfast. Usually the holdfast appears as a thin surrounding film which not infrequently is twice the diameter of the cells themselves. Others have distinct capsules. By observing these from the bottom through cover slips which have been submerged, the capsular material is found to be in intimate contact with the glass over an appreciable area. However, dead or old capsulated species do not adhere to submerged slides in great numbers, which constitutes further proof that periphytes cement themselves to the glass and are not merely mechanically stuck thereto. However, it is not improbable that the electrophoretic properties of the bacteria may influence their initial contact with the glass.

After being washed the slides were stained for five minutes with Conn's rose bengal which consists of 1.0 per cent of the dye and 0.02 per cent CaCl_2 in 5 per cent aqueous phenol solution. They were examined microscopically using a magnification of $980\times$ and the bacteria in each of 100 or more fields were counted. From these direct counts the number of bacteria per square centimeter of glass slide was estimated.

Even after 6 hours submergence in jars of raw lake water at 4°C ., appreciable numbers of bacteria were found on the slides. Table I summarizes the number of bacteria

TABLE I. *Number of bacteria and micro-colonies per sq. cm. of glass slide after different periods of submergence in lake water at different temperatures*

Submergence time	4°C .		15°C .		25°C .	
	Bacteria	Colonies	Bacteria	Colonies	Bacteria	Colonies
6 hours	19,000	0	36,000	0	47,000	0
1 day	77,000	12	214,000	19	160,000	8
2 days	49,000	36	804,000	66	228,000	74
4 days	51,000	92	331,000	180	257,000	293
7 days	86,000	217	516,000	642	343,000	908

and micro-colonies found per sq. cm. of slide after different submergence periods in raw lake water at different temperatures. Micro-colonies are defined as groups of four or more interconnected cells.

The number of bacteria which attach to the glass slides increases rapidly during the first two days, after which there is considerable fluctuation. This latter is attributed partly to the development of micro-colonies in which it is difficult and frequently impossible to estimate the number of cells, and to the occurrence of pleomorphic senescent forms which escape detection. Furthermore even after 24 hours' submergence in the strong brine, the slides commence to show evidence of corrosion especially at the higher temperatures and this makes it difficult to detect all of the bacteria. Also salt crystallizes on the surface of the slides thereby mechanically blocking bacteria from coming in contact with the slide. Crystallization was especially bad in the 4°C . series. However, on the slides of the 4°C . series as well as on the others, micro-colonies were developing, as shown by their greater abundance and larger size on each successive day. This observation is believed to give incontrovertible evidence that bacteria multiply in unmodified lake water even when the latter is saturated with salt.

There are probably several factors besides temperature which influence the attachment of bacteria to submerged slides. Young cells attach more readily than senescent ones. It has not been feasible to estimate what proportion of bacteria in the lake are periphytic but preliminary experiments with a few pure cultures which have been isolated from plates indicate that some species lack the ability to attach themselves to glass slides. In fact, none have been observed which may be regarded as obligate periphytes. According to ZoBell and Allen ('33) not all species of marine bacteria have attachment propensities. These workers also record that the nutrient properties of the water affect

the attachment of bacteria. In nature other variable factors would be operative such as the movement of the water and the motility of the bacteria themselves.

Most if not all of the bacteria found on slides submerged in lake water undoubtedly represent autochthonous species and not merely passive soil or freshwater contaminants. This was demonstrated by inoculating jars of sterile lake water with soil, raw sewage and peptone-enriched sea water. A control jar was inoculated with enough raw lake water previously enriched with peptone to give approximately the same number of bacteria in each jar. After two days few bacteria and no micro-colonies were found on slides submerged in the lake water inoculated with the mixed microflora of soil, sewage or the sea, whereas many bacteria and large micro-colonies appeared on the slides submerged in lake water inoculated with lake microflora. ZoBell, Anderson and Smith¹⁰ find that Great Salt Lake water is distinctly bacteriostatic as well as bactericidal for most non-indigenous bacteria.

FIELD OBSERVATIONS

Sterile chemically-clean slides were submerged in the lake at four different stations along the south-east shore. The locations were selected with deference to their freedom from freshwater or terrigenous pollution. Slides were planted during each month from September 1935 to January 1936, a period of almost negligible land drainage because of the small amount of precipitation and low temperature. The slides were suspended in the lake by means of wooden carriers made with a grooved cleat to support the bottom of the slides and a cord to hold the top of the slides. The entire carrier including the adjacent supporting and anchoring cords was boiled in paraffin. At the sampling station the carriers were sterilized by immersion in hypochlorite solution after which 4 to 12 slides were placed on each carrier with sterile forceps. Beforehand, the slides, wrapped separately in heavy paper, had been heat sterilized.

The slides were submerged for periods of time ranging from 12 hours to 5 weeks. The most satisfactory results were obtained with slides which were exposed to the water for 24 hours. While there were usually more bacteria and especially more and larger micro-colonies on slides after longer periods of submergence, the slides were badly corroded and the accumulation of detritus interfered with the observation of the attached bacteria. Not infrequently the slides were coated with a layer of salt 1 to 4 mm. thick after two weeks' submergence. One set of slides submerged for 30 days 75 feet from shore on the end of the Salt Company pier near Saltair Resort merits special mention. When the slides were harvested the last day of December, 1935, from water having a temperature of 2.1° C. and a density of 1.219, the entire slide carrier was covered with an encrustation of precipitated salt, fully 8 cm. thick. Nevertheless the examination of the salt encased slides revealed the presence of nearly fifty thousand bacteria and over a hundred micro-colonies per sq. cm. of slide. Some of the micro-colonies consisted of twenty or more morphologically identical bacteria.

Aseptic precautions were exercised in harvesting the slides. When removed from the lake some were dried and transferred to slide boxes while others were placed directly into Coplin jars filled with sterile lake water. These latter slides were examined in the laboratory under a cover slip and were kept flooded with water. The low power revealed a comparatively profuse fauna and flora consisting chiefly of diatoms and protozoa. The number far exceeded the number found in a drop of lake water similarly examined.

Without any fixation the air-dried slides were washed in water to remove the salt. Many of them were examined unstained with the high-dry and some with the dark-field microscope. Certain morphological structures were thus detected which were obliterated by the staining procedures. Then one or more slides from each series were stained with Conn's rose bengal and one with Loeffler's methylene blue. Both stains gave satisfactory

¹⁰ ZoBell, C. E., D. Q. Anderson and W. W. Smith. 1937. The bacteriostatic and bactericidal action of Great Salt Lake water. *Jour. Bact.* 33: 253-262.

results. These were examined under the oil immersion lens (980 \times) noting the different morphological types and the arrangement of cells. Many of the slides were stained by Gram using Hucker's ammonium-oxalate crystal violet.

The bacteria and micro-colonies in each of 100 fields or more were enumerated and from these counts the number of bacteria per sq. cm. of slide was calculated. Table II

TABLE II. *Average number of bacteria and micro-colonies per sq. cm. of glass slide after approximately 24 hours' submergence in Great Salt Lake*

Station location	Water density	Bacteria per sq. cm.	Micro-colonies per sq. cm.
N. Bay, Antelope Island	1.220	36,000	700
Pier near Saltair Resort	1.218	183,000	1,100
Black Rock pier	1.217	95,000	290
Fritsch Island pier	1.218	17,000	40

gives the average number of bacteria and micro-colonies which appeared on the slides after approximately 24 hours' exposure to lake water at four different stations. Bacteria in significant numbers were found attached to the slides in every set and most of the slides exhibited definite micro-colonies. Groups of four or more intimately associated and morphologically similar bacteria are considered micro-colonies. Micro-colony formation shows that the lake contains viable bacteria which are capable of multiplication in unmodified lake water.

The majority of the bacteria are small bacilli. A few vibrio-like bacteria appeared, but from the slides one cannot be sure that they are not merely atypical curved rods. Coccoid forms were numerous although there were none which could be termed true cocci. At least nine distinct morphological varieties of bacteria occurred with regularity. Seven of these appeared in micro-colonies on the slides. Other interesting forms were found occasionally. Ovoid rods about 0.8μ wide and 1.0 to 1.4μ long predominated. Second in abundance were slender rods about 0.5μ wide and 2 to 3μ long. Spindle-shaped rods 0.8μ by 2 to 4μ were noted on many of the slides. Most of the other bacteria were rods of varying length and thickness devoid of any marked differentiating characteristics. Large *B. subtilis*-like rods were rarely seen and never in micro-colonies. Of particular interest is a spirochaete resembling the *Cristispira* which has been seen three or four times on three different slides. Sheathed *Leptothrix*-like forms were found on two slides which had been submerged more than four weeks. Other filamentous alga-like forms were observed which probably belong to the Order *Chlamydobacterales* but they were unlike any described representative of this order. Although no sharp demarcation between capsulated and non-capsulated bacteria was discernible, it is estimated that about one-third of the bacteria had distinct capsules. Spores were not definitely identified but structures very suggestive of spores appeared. Less than ten per cent of the bacteria were Gram-positive. Involutionary forms were numerous and they are most disconcerting. Some of the morphological irregularities may be attributed to plasmoptysis which occurs when the halophilic bacteria are treated with freshwater in the washing and staining procedures. However, most of the bizarre forms probably grow that way and it is not improbable that many of them were so bizarre that they were not even recognized as bacteria.

Attempts to obtain photomicrographs of the varied morphological types and arrangements have been disappointing because, in the first place, the salt corrosion of the slides damages the optical properties of the glass, and secondly, even after prolonged submergence in the lake there are only four to eight bacteria per field excluding micro-colonies. The three dimensional grouping of the latter does not lend itself to photographing at high magnifications.

CONCLUSIONS

The attachment of bacteria to sterile glass slides submerged in Great Salt Lake indicates the presence of abundant and varied bacterial flora. Controlled experiments demonstrate that only living bacteria attach themselves to slides in appreciable numbers. This, together with the fact that micro-colonies develop on slides in the lake, indicates that the bacteria are multiplying in the lake and are not merely passive inhabitants. The inability of soil, sewage or marine bacteria to attach to slides in lake water supplies further proof for the latter contention. Most of the lake bacteria are small Gram-negative rods besides other morphological varieties which do not fit into any conventional classification. The direct microscopic procedure offers possibilities for studying the seasonal and geographic distribution of bacteria in the lake.

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SOCIOLOGICAL SUCCESSION

The changes of social relationships which occur among the young-of-the-year bass in a rearing pond are successional in nature and recapitulate stages in the evolution of the development of animal societies. Each type of relationship or *sociological formation*, has well defined characteristics, and the series of formations, here designated the *sociological succession*, may be outlined briefly as follows:

First formation: The primary aggregation of bass fry, integrated by the sight sense as a matter of retaining the primary visual field, the main points of reference in this visual field being other bass fry which move forward.

Second formation: An aggregation of unassociated individuals, held in mutual proximity by the confines of the pond but completely indifferent to each other and lacking any sense of group integration.

Third formation: An aggregation of individuals who exhibit mutual toleration in ordinary activities and automatic mutual cooperation in the quest for food.

Third formation alternate: An aggregation of individuals of whom the majority constitute a group exhibiting mutual toleration and cooperation in finding food while the other individuals remain isolated from each other and from the group and prey upon its members.

Fourth formation (succeeding the third formation alternate): An aggregation of the few predaceous individuals, who, after eliminating most of the prey group while remaining individually isolated, finally grouped together to finish the rest, and thereafter continued to constitute a group which exhibits mutual toleration and automatic cooperation in finding food.

Knowledge of this phenomenon is essential to a program of fish management in bass ponds, because satisfactory crops of bass are obtained from ponds whose populations pass from the Second Formation to the Third Formation while unsatisfactory crops result if the passage is to the Third Formation Alternate. Fish Management in this instance consists of directing the social behavior of a fish population so that succession takes the direction which favors the welfare of the aggregation and subordinates that of the individual.

The sociological history of bass in rearing ponds is given in greater detail to elucidate the above points. In the main, this follows an account already recorded.¹

Newly hatched bass fry lie close together in their nest for about two days, when, their yolk supply being spent, they are able to "swim up" and maintain positions in mid water, and the most prominent feature of the environment of an individual bass fry consists of an abundance of other young bass. The tendency of young bass to school together when first placed in a rearing pool is probably due to attempts to retain the same visual field, in this case, other bass which serve as points of reference which move forward slowly and at approximately the same rate. The primary aggregation of bass in a rearing pond disintegrates when the powers of locomotion increase to the point where the swimming speeds carry them out of each other's visual field. At this time the young bass swim about individually, each apparently regardless of any other, as they feed upon the entomostracans in the pond.

In the Ohio State fish farms, the bass are habituated to dependence upon ground carp meat after they have grown to a length of about one and one-half inches, which they do when about three weeks old. The bass first eats the meat as it sifts apart in the water while slowly dropping toward the bottom, then learns to watch the food coming through the air and swims vigorously to hit it as it touches the water. Finally, the bass learns to associate the coming of the man who casts the food with the coming of the food. When a feeder walks along a low pond levee, he is visible only to the fish within a radius of 25 feet, and when a fish within this zone sees the feeder and is stimulated by the sight to move toward him for food, another bass within sight of the first bass is stimulated to swim after its neighbor. In this way the bass inside the zone of feeder visibility help fish outside of this zone to find food, exhibiting what Allee has called "automatic mutual cooperation."² Presently the bass start swimming from all parts of a pond towards the feeder as soon as he appears, all fish in the pond eat freely together of the available food supply, and may be considered as constituting a cooperative society.

Though all bass fry are equally developed when placed in a rearing pond and all eat freely of the same food supply, they exhibit normal variation in their rates of growth. In some cases the larger individuals presently claim particular individual niches around the pond margin while most of the rest of the fish commence to school together, and as the schooling fish range around the open waters of the pool they pass the niches of the individuals. The claim holders capture smaller bass as the school passes by and this situation prevails for a long time. However, the time may come before the end of the season when there are very few fish remaining in the prey group, and when the predators can no longer satisfy their hunger by waiting in their holdings to prey upon passing fish, they are obliged to leave their niches to go in active search of food. The predators then form a new ranging group, and the smaller individuals are driven to the protection of the vegetational shoals. Finally all small fish are eliminated and the group then turns readily to dependence on an external food supply. The earlier in the season ponds with aggregations of this sort are drained, the more fish of the prey group are salvaged, and the survival percentage is the minimum when the cycle has been completed.

In some cases it is possible to force individual bass who have claimed holdings to give up their attempts at individualism by leading a school of fish which have learned to follow the feeder directly and repeatedly over the area which the individual bass is attempting to protect. In these cases the individuals have given up their holdings and joined the aggregation, but in other cases this has not been possible.

¹ Langlois, T. H. 1936. A study of the smallmouth bass, *Micropterus dolomieu* (Lacepède) in rearing ponds in Ohio. *Ohio Biol. Surv. Bull.* 33: 191-225.

² Allee, W. C. 1931. Animal Aggregations. *University of Chicago Press.*

In some ponds it has been possible to bring about the cessation of cannibalism by transferring to them some bass which had already, in another pond, formed the habit of dependence on the food provided, as these fish continued to depend upon the external food supply and appeared to influence the other bass to do likewise. However, in some cases the fish introduced appeared to adopt the habits of the other bass in the pond and quit taking the food offered.

Allee² states that "A part of the difficulties we have encountered in discussing the rôle of different types of animal aggregations in the evolution of social groupings may be avoided if we recognize that there are many levels of social organization and that these overlap. Among the groups which we may fairly call 'social' there are: (1) those that show their social habit merely through the toleration of the close proximity of other similar individuals in the same restricted space; (2) those that form groups which react more or less definitely as units—the group integration level; (3) those which show physiological division of labor; finally (4), those that show morphologically distinct casts, each associated with some phase of the division of labor."

In the series of types of social organization which leads to a climax formation in the case of bass in a rearing pond, it may be recognized that there is an evolutionary recapitulation. Considered as an organization in process of development toward its upper limit, the earlier types of social relationships are stages of growth, which exhibit (1) temporary primary aggregation resulting from tropistic reactions to the environment; (2) loose integration characteristic of aggregations of individuals which merely show tolerance for each other in a limited space; and (3) relatively stable, closely integrated aggregations, exhibiting automatic mutual cooperation.

Pearse³ cites the increased opportunity for learning as one of the advantages of close association between individuals. The habituation of the bass in a pond to dependence upon the external food supply is accomplished by teaching a few bass which remain assembled in the current at the pond water supply intake to take ground carp flesh, then leading this group as a nucleus around the pond. Other bass join the group and begin eating carp flesh, and by repeating this many times, the group grows until it finally includes all bass in the pond. This is an advantage gained for many individuals by close association with other individuals.

Child⁴ states that "we find the relation of dominance and subordination an essential factor in the progress of social, as of biological organization." This is exemplified in the progress of social organization among the bass in a rearing pond. When some individuals assume proprietorship of particular areas in the pond they exhibit dominance to any other individual fishes which may enter their individual areas, and the intruders exhibit sense of subordination by yielding to their drive and leaving the claims. Although first applied in this way to individual areas, the dominant individuals presently extend their realms to the entire pond area, and merge with other dominant individuals into a group of dominants. When the entire prey group has been eliminated, the predator group turns readily to dependence upon the external food supply, and then may be considered as becoming subordinate to the man who feeds them.

The feeder, who leads the mass of subordinates along the levee, directly and repeatedly over the holding of a dominant bass, and in this way compels the dominant to join the school, is, in effect, reducing a rival dominant to the level of his associates. The dominant bass who refuses to merge his individuality with the other bass, is effectively preventing the feeder from assuming complete dominance. The domination of an aquatic population by a non-aquatic individual is an exceptional instance of an extended habitat.

³ Pearse, A. S. 1926. *Animal Ecology*. McGraw-Hill, New York.

⁴ Child, C. M. 1924. *Physiological Foundations of Behavior*.

Although the sociological succession here described has been observed in the confines of rearing ponds where only bass of equal age are present, and the series of formations described are those occurring during the passage of a single season (May through October), it is certain that comparable though more complicated succession takes place wherever waters contain fish. Any program of fisheries management which fails to consider this aspect of the problem is probably as doomed to failure as a program of bass rearing in ponds which fails to consider bass cannibalism. A successful fish management program must be based upon methods of utilizing knowledge of and regulating fish behavior.

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THIRTY YEARS OF CHANGE IN DESERT VEGETATION

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The plant communities of the warmer and less arid parts of the American desert are made up of species which differ greatly in morphological and anatomical type, and likewise in length of life, seeding habits, germination, establishment, rate of growth, and sensitiveness to adverse environmental conditions. The cohabitation of plants in which these features are often widely dissimilar results in a constant shifting in the size and composition of the plant population of small areas. Observation of changes in vegetation over long periods is calculated to throw light on the ecological behavior of the species concerned, and to determine developmental trends in the vegetation.

The aim of this paper is to give the history of the changes in vegetation that have taken place on 14 areas on the grounds of the Desert Laboratory, at Tucson, Arizona. A previous paper¹ by the senior author described the condition of 6 of these areas in 1928. Five areas 100 m. square were mapped by the late Prof. Volney M. Spalding in 1906, being designated S 11, S 12, S 15, S 16 and S 17. (The other areas in his series were not germane to this investigation.) Two of these were re-mapped in 1910 and all of them in 1928 and 1936. An area of 557 sq. m. was enumerated in 1910, 1928 and 1936 but has never been mapped. In 1928 a group of 8 contiguous areas 10 m. square was established and mapped and was re-mapped in 1936, these being designated B 1, B 2, B 3, B 4, B 5, B 6, B 7, and B 8.

The grounds of the Desert Laboratory were fenced in 1907 and have been continuously protected from grazing and trespass since then. Prior to the fencing there had been light or moderate grazing of the area by horses, cattle and burros turned loose by the inhabitants of Tucson, two miles distant. It is probable that the amount of grazing was not great enough to disturb seriously the larger plants but was enough to reduce the grasses and smaller perennials far below their normal numbers. It seems certain that many of the changes in the vegetation since 1906 consist largely in the return of the vegetation from a somewhat disturbed state toward a condition which gradually approaches the primeval one. This is indicated in the general increases in

¹ Shreve, Forrest. 1929. Changes in desert vegetation. *Ecology* 10: 364-373.

plant population and particularly in the larger number of grasses and of palatable plants such as *Menodora scabra* and *Calliandra eriophylla*.

In 1928 it was found that a very considerable increase had taken place since 1906 in the number of plants on the older areas. It was felt at that time that the vegetation had come close to reaching its original density. The examination in 1936 has shown that this is not the case. The total population of the 5 Spalding areas in 1906 was 531 and in 1928 was 739. In 1936 their total was found to be 1,401. In other words, the increase during the first 22 years of protection was greatly exceeded in the subsequent 8 years. There is nothing in the annual fluctuations of rainfall to explain this and the facts are manifestly due to the slowness with which proper conditions are built up for the successful establishment of larger numbers of young plants.

The areas here described are marked by metal rods set in concrete but are not separately enclosed. They are not protected from the numerous small rodents, which must be regarded as part of the natural environment of the plants. The method of mapping consists in driving wooden pegs at 1 m. intervals around the area and stretching stout white cord between the pegs so as to lay out the entire area in one meter squares. Mapping is done on coordinate paper on which the meter squares are divided into tenths. The position of the plants is either estimated or measured with a meter stick. The position of small plants is indicated by an appropriate symbol or by a dot with the initials of the plant. For larger plants a dot is placed at the location of the crown of the root and a circle is drawn to show the spread of the branches.

The enumeration of plants has been confined to perennials, including all small shrubs and bushes which persist from season to season with shoots or crown above the soil. It has not included bulbous perennials or root perennials which are not discoverable in the dry months, such as *Delphinium scaposum* and *Anemone sphenophylla*. All of the enumerations have been made in dry months in order to avoid the heavy growth of annuals which makes the visibility of the small perennials poor. Small plants of the perennials have been enumerated whenever it was certain that they were alive. Plants which grow in mats and multiply by prostrate branches, as *Calliandra eriophylla* and *Coldenia canescens* have been mapped so as to indicate as an individual each crown from which several branches radiate. Even in enumerations made at the same season it is difficult to eliminate errors which may arise from great variation in visibility and manifestations of life, due to the rainfall and temperature conditions of the one or two preceding growing seasons. This source of error accounts for the erratic statistics for *Sphaeralcea grossulariaefolia pedata*, *Verbena gooddingii nepetifolia* and *Ayenia pusilla*.

The fluctuations of population could be followed much more closely by making annual enumerations of the areas, and close correlation of the fluctua-

tions with seasonal conditions could then be made. It has seemed desirable, however, to defer annual mapping until the vegetation gives evidence of having more completely recovered from disturbance. Frequent mapping is, in fact, undesirable on account of the serious disturbance of plants and soil surface which inevitably results.

In certain parts of the grounds of the Desert Laboratory there has been a marked increase in the stand of grasses during the past 20 years. This is particularly true of *Hilaria mutica* on the upper slopes of Tumamoc Hill and *Muhlenbergia porteri* on the lower slopes and parts of the adjacent bajada. It happened that the Spalding areas were all laid out in spots where there were very few perennial grasses during the period from 1906 to 1928. The location selected in 1928 for the areas in series B was chosen on account of the sparsity of large perennials and the indications that the conditions existing there were favorable for ultimate development of grasses. In 1936 grasses were found to have invaded four of the Spalding areas and to have appeared to a greater or less extent in 5 of the 8 areas in series B. In mapping it has been found more satisfactory to indicate the areas covered by grasses than to attempt to count the individual tufts. It must be noted, therefore, that the grasses are not included in the population statistics, and that including them would greatly increase the figures for the 1936 population of areas S 12, B 1, B 2, B 3, B 4, and B 7.

AREAS ESTABLISHED IN 1906

In tables I to V are given the statistics for the plant population of the five Spalding areas, together with figures for the number of deaths and additions for each species during the intervals between enumerations.² It will be noted that each of the areas examined in 1910 (S 11 and S 15) showed a reduction of population for the four years following the first charting. In S 11 this was mainly due to the disappearance of *Abutilon crispum* and *Notholaena hookeri*, neither of which has reappeared in the area. In S 15 it was largely due to deaths in *Janusia*, *Calliandra* and *Menodora*, all of which had again increased to much larger numbers by 1928. It is highly probable that the reduction in the number of these three species, and smaller reductions in others, was due to the death of mature plants and the failure of seedlings to become established under conditions which were still unfavorable for reproduction. The results of the disturbance of natural conditions by grazing naturally persisted for several years after the grounds were fenced. The most important requirement for good reproduction is the existence of small but dense colonies of bushes, usually in the partial shade of the larger perennials, and the accumulation of fallen twigs and leaves as well as the dead annuals of preceding years. The destruction or impairment of these natural seeding beds would first be registered in the figures for population after a

² Readers who are interested in seeing the maps of the areas described in this paper will be supplied with photostatic copies on application to the authors.

period of several years. Some features of the difference between the conditions in the open and under the shade of a large *Cercidium* tree have been described by the senior author³ on the basis of work done on the grounds of the Desert Laboratory.

TABLE I. *Record of changes in plant population on area S 11*

	Population, 1906	Population, 1910	Deaths	Additions, 1910- 27	Population, 1928	Deaths	Additions, 1928- 35	Population, 1936
<i>Carnegiea gigantea</i>	2	2	1	0	1	0	0	1
<i>Cercidium microphyllum</i>	2	2	0	1	3	0	1	5
<i>Fouquieria splendens</i>	1	1	1	0	0	0	0	0
<i>Lycium berlandieri</i>	10	11	2	2	11	0	0	11
<i>Janusia gracilis</i>	6	9	5	9	13	1	5	17
<i>Encelia farinosa</i>	80	83	81	79	81	47	112	146
<i>Jatropha cardiophylla</i>	1	1	0	3	4	0	0	4
<i>Lippia wrightii</i>	0	0	0	1	1	1	0	0
<i>Menodora scabra</i>	0	0	0	2	2	1	0	1
<i>Verbena gooddingii nepetifolia</i>	3	0	0	0	0	0	0	0
<i>Franseria deltoidea</i>	0	0	0	0	0	0	1	1
<i>Haplophyton cymicidium</i>	0	0	0	0	0	0	2	2
<i>Abutilon crispum</i>	17	0	0	0	0	0	0	0
<i>Sphaeralcea grossulariaefolia</i> <i>pedata</i>	1	0	0	0	0	0	3	3
<i>Abutilon incanum</i>	4	0	0	0	0	0	0	0
<i>Brickellia coulteri</i>	0	0	0	0	0	0	2	2
<i>Notholaena hookeri</i>	9	0	0	0	0	0	0	0
Totals	136	109	90	97	116	50	127	193

Area S 11 (table I) is located about 150 m. southwest of the main building of the Desert Laboratory on a west-facing slope with a gradient of 15° to 25°. The soil is shallow and the surface strewn with basaltic rocks. Between 1910 and 1928 there was an increase of population of 28 per cent, and between 1928 and 1936 an increase of 66 per cent. Five species represented in 1906 are absent in 1936, while four new species have appeared in the same period. One shrub, *Lippia wrightii*, which is abundant on nearby slopes, appeared for the first time in 1928 with a single individual but it has not persisted. In 1928 few of the species had shown much increase over 1910. The principal part of the increase between 1928 and 1936 is on the part of *Encelia farinosa*. In 1906 there was a single tuft of the grass *Bouteloua rothrockii*, while in 1936 there are 12 tufts of this grass and *Hilaria mutica*.

The principal interest of area S 11 is in connection with the behavior of the composite shrub *Encelia farinosa*, which is an important component of the vegetation of hills and mountain slopes throughout southern Arizona. It has been the dominant species of this area, and of much of the adjacent ground, since the first mapping in 1906. Between 1906 and 1910 it lost one

³ Shreve, Forrest. 1931. Physical conditions in sun and shade. *Ecology* 12: 96-104.

also gained a new individual, thereby maintaining its population of 83 plants over a period of 4 years. This record indicates that all but one were more than four years old in 1910. At the time of the third mapping, in 1928, 81 of the plants had died, leaving only two of those that were present in 1910. One of these was a relatively younger plant but the other had persisted apparently from the first record in 1906, a period of 22 years. Seventy-nine additions appeared between 1910 and 1928, nearly balancing the loss of 81 plants. In 1928 the *Encelia* plants were mostly young. During the following 7 years up to 1936, 47 of the 81 individuals died, while there were 112 new appearances, making an increase of more than 80 per cent. The present population of *Encelia* is 146 on this area. The original total of 83 plants in 1906 has nearly doubled within 30 years. Over the 18-year period the original population very nearly maintained a balance. These figures offer no evidence of a regular periodical increase, but they indicate likeliness to persist and to increase. There seems to be some correlation between the rate of increase and the amount of rainfall for the year preceding mapping, as shown in the table below. The average annual rainfall is approximately 11 inches.

Year of mapping	1910	1928	1936
Change in population for period preceding	Balance	2.4% decrease	80.2% increase
Rainfall for year preceding	12.32 in.	10.58 in.	15.60 in.

Over one period of 4 years the individuals of *Encelia* persisted with a single loss; over a period of 17 years the population was maintained by a nearly complete stand of new individuals; over a period of 8 years somewhat more than half of the individuals perished concurrently with the appearance of a larger number of new ones. The average length of life of *Encelia* is uncertain from these statistics, but probably lies between 6 and 12 years. At least one exceptionally long-lived individual appears to have persisted 22 years.

Area S 12 (table II) is located about 400 m. southwest of the Laboratory, on an east-facing slope with a gradient of 10 to 15°. The soil is shallow and only a small percentage is covered by large rocks. At the present time the preponderant plants in this area are *Janusia gracilis*, *Menodora scabra* and *Sphaeralcea grossulariaefolia pedata*. The population fell from 166 in 1906 to 143 in 1929, chiefly due to the heavy loss in *Sphaeralcea*. In this period *Fouquieria* disappeared and five new species appeared, including four individuals of *Encelia*, which plays a very unimportant rôle in the area. The principal gain in the 23 years was made by *Janusia gracilis*. During the last 7 years there has been a net increase of 64 per cent in the total population. *Janusia* has continued the gain which it made in the first period, *Menodora* has more than recovered its loss during the first period, and *Sphaeralcea* has again risen to an important position after having fallen to two individuals in 1929. *Encelia* and *Ephedra* have again disappeared from the vegetation.

TABLE II. *Record of changes in plant population on area S 12*

	Popu- lation, 1906	Deaths, 1906- 29	Addi- tions, 1906- 29	Popu- lation, 1929	Deaths, 1929- 35	Addi- tions, 1929- 35	Popu- lation, 1936
<i>Cercidium microphyllum</i>	4	1	0	3	0	0	3
<i>Fouquieria splendens</i>	1	1	0	0	0	0	0
<i>Acacia paucispina</i>	6	2	1	5	0	1	6
<i>Lycium berlandieri</i>	2	0	2	4	0	3	7
<i>Opuntia versicolor</i>	12	10	1	3	1	5	7
<i>Janusia gracilis</i>	8	6	59	61	2	31	90
<i>Encelia farinosa</i>	0	0	4	4	4	0	0
<i>Lippia wrightii</i>	10	3	2	9	0	1	10
<i>Olneya tesota</i>	0	0	1	1	0	0	1
<i>Ferocactus wislizeni</i>	0	0	1	1	0	0	1
<i>Menodora scabra</i>	65	62	43	46	20	45	71
<i>Sphaeralcea grossulariaefolia pedata</i>	58	58	2	2	2	33	33
<i>Ephedra trifurca</i>	0	0	1	1	1	0	0
<i>Tragia ramosa</i>	0	0	3	3	2	3	4
<i>Opuntia phaeacantha</i>	0	0	0	0	0	1	1
<i>Hibiscus coulteri</i>	0	0	0	0	0	1	1
Totals	166	143	120	143	32	124	235

Fouquieria has not reappeared, and only two species have entered the area since 1929. A strong contrast is afforded between *Janusia* and *Menodora* with reference to duration of life. In 23 years 6 of the original 8 plants of *Janusia* died but during the succeeding 7 years only 2 died out of a population of 61. In *Menodora* 62 of the original 65 perished in the 23 year period, and during the subsequent 7 years 20 died out of the population of 46. There is a strong indication here that the average life of *Menodora* is not greater than 15 years and that of *Janusia* probably well above 20 years.

Area S 15 (table III) is located 1,150 m. west of the Desert Laboratory on a nearly level basaltic outcrop provided with soil from 15 to 35 cm. in depth. In 1906 the population of this area was 101 plants and 15 species were represented; in 1910 the population was 48 plants in 11 species; in 1928 142 plants in 14 species; and in 1936 440 plants in 20 species. Of the last number 286 are *Franseria deltoidea* and *Calliandra eriophylla*. In 1906 the predominant plant was *Janusia*, which has now fallen to a secondary place with a very small increase from 28 to 30 plants. Between 1906 and 1910 *Calliandra* and *Menodora* suffered heavy losses and *Franseria* nearly maintained its numbers. Between 1910 and 1928 *Janusia*, *Calliandra*, *Menodora* and *Franseria* made heavy gains. During the last 8 years *Calliandra* and *Franseria* have each gained over 300 per cent, *Janusia* has gained about 30 per cent and *Menodora* has lost one more individual than it has gained. Plants not represented in 1906 which are now prominent are *Porophyllum gracile* and *Ayenia pusilla*. The former appeared in 1928 with 9 individuals, now increased to 40, and the latter first appeared in the enumeration of 1936

TABLE III. *Record of changes in plant population on area S 15*

	Popu- lation, 1906	Popu- lation, 1910	Deaths, 1910- 27	Addi- tions, 1910- 27	Popu- lation, 1928	Deaths, 1928- 35	Addi- tions, 1928- 35	Popu- lation, 1936
<i>Carnegiea gigantea</i>	3	3	0	0	3	0	1	4
<i>Cercidium microphyllum</i>	7	7	2	1	6	1	0	5
<i>Larrea tridentata</i>	1	1	0	0	1	0	0	1
<i>Fouquieria splendens</i>	0	0	0	1	1	0	0	1
<i>Acacia paucispina</i>	1	1	0	0	1	0	0	1
<i>Lycium berlandieri</i>	0	0	0	2	2	0	0	2
<i>Opuntia leptocaulis</i>	3	1	0	1	2	0	4	6
<i>Neomammillaria microcarpa</i>	0	0	0	1	1	1	1	1
<i>Janusia gracilis</i>	28	3	1	21	23	3	10	30
<i>Calliandra eriophylla</i>	14	3	0	21	24	9	102	117
<i>Encelia farinosa</i>	1	2	2	1	1	1	3	3
<i>Riddellia cooperi</i>	4	4	4	0	0	0	0	0
<i>Menodora scabra</i>	10	5	3	26	28	6	5	27
<i>Porophyllum gracile</i>	0	0	0	9	9	2	33	40
<i>Franseria deltoidea</i>	19	18	11	33	40	8	137	169
<i>Sphaeralcea grossulariae- folia pedata</i>	2	0	0	0	0	0	4	4
<i>Ayenia pusilla</i>	0	0	0	0	0	0	13	13
<i>Krameria canescens</i>	0	0	0	0	0	0	5	5
<i>Opuntia phaeacantha</i>	0	0	0	0	0	0	1	1
<i>Opuntia versicolor</i>	1	0	0	0	0	0	0	0
<i>Isocoma hartwegi</i>	3	0	0	0	0	0	0	0
<i>Philibertia hartwegi</i>	0	0	0	0	0	0	0	0
<i>Carlownrightia arizonica</i>	0	0	0	0	0	0	0	0
Totals	97	48	23	117	142	31	329	440

with 13 individuals. In 1936 some 16 tufts of perennial grasses had appeared in the southeastern corner of this area.

Area S 16 (table IV) is located about 100 m. northwest of area S 15, on level ground with deep rhyolitic outwash soil and a surface covered with very small rock fragments. The area is typical of the open bajada vegetation in which *Larrea tridentata* is the dominant plant. In 1906 this area was largely bare, with only 27 perennials in 6 species. At that time there were 16 individuals of *Larrea*, a number which has fallen to 13 in 1936, at the same time that the total population has risen to 224. At present the predominant plant is *Krameria canescens*, which has increased from 5 to 76 individuals in 30 years. *Coldenia canescens* has increased from 2 plants to 37 in the same period. *Franseria deltoidea* was not represented in 1906 but was the predominant species in 1928, with 35 individuals, and now has 52. *Riddellia cooperi* was absent in 1906 and 1928 but has now invaded the area with 31 individuals. Two of the large perennials, *Fouquieria* and *Acacia*, disappeared from the area between 1906 and 1928, so that there are only four species common to the lists of 6 species present in 1906 and 11 in 1936.

Area S 17 (table V) is located about 200 m. southwest of area S 15, on level ground near an abrupt descent of 4 m. The soil and surface are similar to those of the preceding area. In 1906 S 17 was similar to S 16 in its small

TABLE IV. *Record of changes in plant population on area S 16*

	Popu- lation, 1906	Deaths, 1906- 27	Addi- tions, 1906- 27	Popu- lation, 1928	Deaths, 1928- 35	Addi- tions, 1928- 35	Popu- lation, 1936
<i>Larrea tridentata</i>	16	2	0	14	1	0	13
<i>Fouquieria splendens</i>	1	1	0	0	0	0	0
<i>Acacia paucispina</i>	2	2	0	0	0	0	0
<i>Krameria canescens</i>	5	0	9	14	0	62	76
<i>Opuntia leptocaulis</i>	1	0	3	4	0	1	5
<i>Echinocereus fendleri</i>	0	0	1	1	0	0	1
<i>Calliandra eriophylla</i>	0	0	1	1	0	0	1
<i>Franseria deltoidea</i>	0	0	35	35	8	25	52
<i>Coldenia canescens</i>	2	2	0	0	0	37	37
<i>Cercidium microphyllum</i>	0	0	0	0	0	1	1
<i>Zinnia pumila</i>	0	0	0	0	0	6	6
<i>Riddellia cooperi</i>	0	0	0	0	0	31	31
<i>Ayenia pusilla</i>	0	0	0	0	0	1	1
Totals	27	7	49	69	9	164	224

TABLE V. *Record of changes in plant population on area S 17*

	Popu- lation, 1906	Deaths, 1906- 27	Addi- tions, 1906- 27	Popu- lation, 1928	Deaths, 1928- 35	Addi- tions, 1928- 35	Popu- lation, 1936
<i>Cercidium microphyllum</i>	1	0	0	1	0	0	1
<i>Acacia paucispina</i>	5	2	0	3	1	0	2
<i>Lycium berlandieri</i>	1	1	0	0	0	1	1
<i>Krameria canescens</i>	1	1	1	1	0	0	1
<i>Opuntia fulgida</i>	6	5	1	2	1	4	5
<i>Calliandra eriophylla</i>	1	1	0	0	0	0	0
<i>Riddellia cooperi</i>	6	6	0	0	0	0	0
<i>Echinocereus fendleri</i>	0	0	1	1	1	0	0
<i>Crassina pumila</i>	11	11	4	4	3	0	1
<i>Franseria deltoidea</i>	55	48	250	257	8	41	290
<i>Sphaeralcea pedata</i>	2	2	0	0	0	0	0
<i>Neomammillaria microcarpa</i>	0	0	0	0	0	1	1
Totals	89	77	257	269	14	47	302

flora and small number of large perennials. The cover was much heavier, however, owing to the presence of 55 individuals of *Franseria* and 11 of *Zinnia pumila*. In 1928 *Franseria* had increased to 257, but the total additional population had fallen from 34 to 12. In 1936 *Franseria* had risen to 290 and the total number of its associates had remained at 12. The number of species on the area was 10 in 1906 but has fallen to 8 at the present time.

The charts of the 5 Spalding areas made in 1906 indicate the occurrence of grasses only on S 11, where there was one plant of *Bouteloua rothrockii*, and on S 15, where 4 plants of *Aristida orcuttiana* were shown. In 1928 the grasses were not mapped, although their appearance on S 12 was noted. In

1936 the individual tufts or areas of the perennial grasses were mapped. The word "tuft" indicates in some cases a single vigorous plant and in other cases a small compact group of plants. In the larger patches of grass the number of tufts or individuals was not counted. On S 11 there were 12 tufts, occupying less than .5 sq. m. On S 12 there were 67 tufts or small areas occupying about 11 sq. m. On S 15 there were 15 tufts, with a total area of less than .5 sq. m. On S 16 there were no grasses. On S 17 there were 56 tufts occupying about 1.5 sq. m. On the group of areas the total number of tufts in 1936 was 150 and their combined area was not greater than 13.5 sq. m., or 2.7 per cent of the entire surface.

The most striking feature of the 30-year comparison of the Spalding areas is the increase in their total plant population from 530 to 1,401 individuals, and the fact that all of the areas shared in the increase. The percentage of increase for the several areas was as follows: S 11, 75 per cent; S 12, 42 per cent; S 15, 851 per cent; S 16, 730 per cent; and S 17, 240 per cent. A greater increase was found both in 1928 and in 1936, in the last three areas, situated on level ground, than in the first two, situated on the slopes of Tumamoc Hill. This seems to be explainable only on the likelihood that the level part of the Laboratory Grounds suffered more from grazing prior to 1907 than the rugged hillside did.

TABLE VI. *Record of changes in plant population on area A*

	1910	1928	1936
<i>Carnegiea gigantea</i>	2	3	2
<i>Cercidium microphyllum</i>	22	21	21
<i>Acacia paucispina</i>	10	11	12
<i>Laurea tridentata</i>	24	22	26
<i>Fouquieria splendens</i>	6	6	5
<i>Opuntia versicolor</i>	9	8	8
<i>Opuntia phaeacantha</i>	3	5	5
<i>Lycium berlandieri</i>	3	5	10
<i>Ferocactus wislizeni</i>	1	2	2
<i>Krameria canescens</i>	2	2	2
<i>Jatropha cardiophylla</i>	0	1	1
Totals	82	86	94

It is obvious from an examination of the foregoing tables that the great increases of population have been made mainly by certain smaller and relatively short-lived perennials, and that the change in numbers has been very small on the part of the larger perennials which dominate the physiognomy of the vegetation. In table IX are given the total numbers of 6 large perennials on all of the Spalding areas and the totals for 5 small perennials. A striking contrast is seen between the increase of nearly 250 per cent on the part of the small perennials and the net loss of one individual in the group of 66 large perennials. The small perennials spring up in large numbers and their presence is largely a function of the moisture conditions of the one

or two preceding years, as shown above for *Encelia* in area S 11. The large perennials give rise to fewer seedlings and the conditions for their permanent establishment are far more exacting. After the approximate restoration of natural conditions in all of the areas, the succeeding enumerations will doubtless show great fluctuations in the numbers of the small perennials and smaller and slower fluctuations among the large perennials.

AREAS ESTABLISHED IN 1910 AND 1928

Area A is a slightly irregular rectangle of 557 sq. m. situated on a gently sloping part of the north face of Tumamoc Hill 120 m. north of the main building of the Desert Laboratory. This area has never been mapped but the large perennials were enumerated in 1910, 1928, and 1936, with the figures resulting which are shown in table VI.

There has been a small progressive increase in the totals for area A, due to *Lycium Berlandieri* more than any other plant. None of the species present in 1910 have disappeared and only one, *Jatropha cardiophylla*, has appeared. Three of the original ten species have suffered a small loss, two have made no change, and five have increased.

Areas B 1 to B 8 were first surveyed and mapped in 1928 and were given their first subsequent examination in 1936. The eight areas, each 100 m. square, are merely subdivisions of an area of 200 by 400 m. The location is 530 m. northeast of the southwest corner of the Desert Laboratory grounds, on a slightly rolling surface with a light loam soil and without the mulch or pavement of stones found on all of the older areas. The location was selected because it differs greatly from all of the others in the texture and structure of its soil and in the openness and poverty of its vegetation. It gave the impression in 1928 of having changed little in the 21 years that it had been protected, although similar ground for 800 m. to the north of it had shown a steady increase in its stand of perennial grasses.

In table VII are given the data for the collective populations of the eight 100 meter squares in 1928 and 1936, together with the number of deaths and new establishments in each species. In 1928 there were 18 species represented, to which 5 species were added in the period between examinations. None of the species originally present disappeared during the 8 years. Out of the original population of 163 plants there were 34 deaths. The number of new plants found in 1936 was 337, raising the total to 466, an increase of 350 per cent. There were deaths in 8 of the original species, and additions in 12 of them. *Fouquieria*, *Atriplex canescens*, and *Opuntia versicolor* are the only species in which there was no change.

A large part of the increase found in 1936 is due to the appearance of 197 young individuals of *Aplopappus hartwegi*. Of this number 152 are grouped under the light shade of a *Prosopis* tree which covers 40 sq. m. The remaining 45 plants are more or less evenly distributed over the other parts of area B. This species of *Aplopappus* is extremely abundant in the Tucson

TABLE VII. *Record of changes in plant population on areas B 1 to B 8*

	Popula- tion, 1928	Deaths, 1928-35	Addi- tions, 1928-35	Popula- tion, 1936
<i>Riddellia cooperi</i>	1	0	7	8
<i>Aplopappus Hartwegi</i>	0	0	197	197
<i>Opuntia fulgida</i>	14	6	25	33
<i>Acacia paucispina</i>	2	1	0	1
<i>Franseria deltoidea</i>	29	6	36	59
<i>Echinocereus fendleri</i>	6	4	0	2
<i>Krameria canescens</i>	27	7	16	36
<i>Krameria glandulosa</i>	4	0	2	6
<i>Larrea tridentata</i>	46	2	14	58
<i>Opuntia leptocaulis</i>	11	2	15	24
<i>Opuntia spinosior</i>	5	2	6	9
<i>Zinnia pumila</i>	0	0	7	7
<i>Opuntia phaeacantha</i>	5	3	3	5
<i>Atriplex canescens</i>	1	0	0	1
<i>Ephedra trifurca</i>	3	0	2	5
<i>Opuntia versicolor</i>	1	0	0	1
<i>Fouquieria splendens</i>	3	0	0	3
<i>Neomammillaria microcarpa</i>	2	0	2	4
<i>Prosopis velutina</i>	2	0	1	3
<i>Ferocactus wislizeni</i>	0	0	1	1
<i>Cercidium microphyllum</i>	0	0	1	1
<i>Carnegiea gigantea</i>	1	1	1	1
<i>Lycium berlandieri</i>	0	0	1	1
Totals	163	34	337	466

region and is known to have multiplied greatly in the last 25 years, presumably as an indirect effect of over-grazing. It is not common on the Laboratory grounds and there will be considerable interest in learning from the future study of this area whether it multiplies under natural conditions. Without the appearance of *Aplopappus* the increase in population would have been only 66 per cent.

During the 8 year period substantial gains were made by *Larrea* and *Franseria deltoidea*, two of the most abundant plants of the surrounding area, and by *Opuntia fulgida* and *O. leptocaulis*, which multiply by fallen joints much more often than by seed. The rest of the list shows small gains, distributed among the larger long-lived perennials *Ephedra*, *Prosopis*, *Cercidium*, *Krameria canescens*, and *Lycium* and the smaller short-lived ones *Riddellia* and *Zinnia*. Among the 9 species of cacti represented on the areas at present, 1 has decreased, 3 have not changed, and 5 have increased.

In 1928 there were 21 small tufts of perennial grasses on the 8 areas in B, covering collectively less than 1 sq. m. In 1936 there were tufts, chiefly *Aristida orcuttiana* and *Bouteloua rothrockii*, on 112 of the 800 individual square meters laid off for mapping, and it was estimated that the total area covered by them, if they were assembled so that the leaves made a continuous ground cover, would be about 31 sq. m. or 3.8 per cent of the total area. The actual number of individual tufts was probably about 7,000. The steady increase in grass cover throughout the grounds during the past 15 years,

TABLE VIII. *Total plant population of observational areas at Desert Laboratory on the years indicated*

Area	1906	1910	1928	1936
S 11	136	109	116	193
S 12	166	—	143	235
S 15	97	48	142	440
S 16	27	—	69	224
S 17	89	—	269	302
A	—	82	86	94
B 1	—	—	43	67
B 2	—	—	40	60
B 3	—	—	20	36
B 4	—	—	16	37
B 5	—	—	13	36
B 6	—	—	10	182
B 7	—	—	9	19
B 8	—	—	12	29
Total population by groups of areas				
S 11, S 15	233	157	258	633
S 12, S 16, S 17	282	—	481	761
B 1 to B 8	—	—	163	466
Comparable totals			902	1860

especially on the slopes of Tumamoc Hill and near its base, has involved the above species and *Hilaria mutica*, *Muhlenbergia porteri*, *Heteropogon contortus*, *Aristida ternipes* and other species. There is every reason to anticipate that the grass cover on this series of areas will become greater during the next 10 years rather than less.

LENGTH OF LIFE

The detailed statistics for the six large perennials (in tables I to V) show that 21 individuals died and 20 new individuals appeared in an original population of 66. Over a 30 year period the number of deaths was approximately one-third of the total number of these plants. This may be taken as giving some indication that the average length of life of these six species is about 90 years. It has been found⁴ that the average length of life of *Carnegiea* is well above 100 years and that it may be as great as 175 years in favorable habitats. In *Cercidium microphyllum* (*Parkinsonia microphylla*) it has been found⁵ that approximately two-thirds of the individuals in a normal stand of this tree are 200 years old or more. Measurements of the growth of *Ferocactus wislizeni* made over a period of 25 years indicate a normal length of life of about 130 years.⁶ Photographic records have been kept of a number of large individuals of *Larrea* in the vicinity of the Desert

⁴ Shreve, Forrest. 1910. The rate of establishment of the giant cactus. *Plant World* 13: 235-240.

⁵ ———. 1911. Establishment behavior of the palo verde. *Plant World* 14: 289-296.

⁶ ———. 1935. The longevity of cacti. *Cac. and Succ. Jour.* 7: 66-68.

Laboratory for 30 years. The largest ones have undergone little change in size and bulk in that period. Similar individuals have been uprooted in the vicinity and showed heavy root crowns 16 to 20 in. in diameter from which numerous branches had arisen which no longer formed a part of the plant. In the absence of direct evidence it seems safe to infer that large individuals are generally well in excess of 100 years of age. The rate of growth and the mortality of *Fouquieria* are high and it is doubtful if its average length of life is greater than 60 years. No evidence is available on the length of life of *Acacia paucispina* and *Lycium berlandieri*. However the indication of the proportion of deaths to total population on the Spalding areas is in general agreement with direct evidence to the effect that 90 years is close to the average length of life of the six large perennials listed in table IX. There

TABLE IX. Comparative totals for changes in number of large perennials and selected small ones on the 5 Spalding areas

Large perennials	1906	1928	1936
<i>Carnegiea gigantea</i>	5	4	5
<i>Cercidium microphyllum</i>	14	11	15
<i>Fouquieria splendens</i>	3	1	1
<i>Acacia paucispina</i>	14	9	9
<i>Larrea tridentata</i>	17	15	14
<i>Lycium berlandieri</i>	13	17	21
Totals	66	57	65
Small perennials			
<i>Encelia farinosa</i>	81	86	149
<i>Franseria deltoidea</i>	74	332	512
<i>Menodora scabra</i>	75	76	99
<i>Janusia gracilis</i>	42	97	137
<i>Krameria canescens</i>	6	15	82
Totals	278	606	979

is evidence that at least some individuals of *Calliandra eriophylla*, *Encelia farinosa*, *Franseria deltoidea*, *Janusia gracilis* and *Coldenia canescens* have lived to an age of 22 years, but this appears to be an unusual age for *Encelia* and *Franseria*. *Menodora scabra* often lives more than 7 years but rarely 18 to 22. *Porophyllum gracile* and *Riddellia cooperi* live at least 7 years, and *Sphaeralcea grossulariaefolia pedata* usually a shorter period than that.

FLORISTIC CHANGES

Table X has been drawn up to indicate the changes in the number of species of perennials represented on the areas during the period of observation. The changes in number of species have in some cases followed those in the number of individuals. On S 11 and S 15 there was a decline between 1906 and 1910 in number of species and number of individuals. During the period from 1906 to 1928 there was a general increase in the number of individuals but the number of species declined on S 11 and S 17 and re-

TABLE X. Number of species of perennial plants represented on observational areas at Desert Laboratory on the years indicated

Area	1906	1910	1928	1936
S 11	12	7	8	11
S 12	9	—	13	13
S 15	14	11	14	20
S 16	6	—	6	11
S 17	10	—	7	8
A	—	10	11	11
B 1-B 8	—	—	18	23

mained the same on S 15 and S 16. Between 1928 and 1936 there was a small increase in the number of species on all of the areas except S 12 and A.

All of the increases in the number of species found on the areas are due to the appearance of plants already represented on other areas or on the intervening ground (except in the case of *Aplopappus hartwegi*). The increases are therefore merely an expression of the local movements of these species and an indication of a trend toward the more uniform representation of all of them throughout the larger area in which the observational plots are located. Such a trend is apparently in constant operation and is continually being held in check by the unsuitable habitat conditions which the disseminated plants sometimes encounter.

TRENDS OF CHANGE

In a type of vegetation which is made up of both large and small plants it is naturally the large ones which do most to determine the physiognomy. Since it is likewise the large plants which have the greatest length of life it follows that substantial changes in the visibly dominant species are registered only at a very slow rate. This is illustrated by the fact that there has been a change of only 1 in the number of large perennials on 500 sq. m. in 30 years.

At the same time there have been significant changes in the number of smaller plants, which are usually numerically dominant. In table XI are shown the numerical dominants in the 5 Spalding areas and areas A and B 1 to B 8. On 3 of the oldest areas the dominance was held by the same plant throughout the 30-year period. On area S 12 the dominance was shifted once and on S 16 was shifted twice. On the 9 remaining areas dominance was held on 4 and shifted on 5.

The history of all of the areas shows that the newly established individuals have, with one exception, belonged to species which previously grew on the area or else on adjacent ground. The changes of dominance have frequently been merely the shifting of a plant from second or third place to first place, and perhaps without any change in the number of the plant thus thrown into second place. *Larrea* fell from first to second or third place in areas B 1, B 4, B 5, B 6, and B 8, at the same time that its numbers increased on all but

TABLE XI. Showing the numerically dominant species in 14 observational areas on the years indicated

Area	1906	1928	1936
11	<i>Encelia farinosa</i>	<i>Encelia farinosa</i>	<i>Encelia farinosa</i>
12	<i>Menodora scabra</i>	<i>Janusia gracilis</i>	<i>Janusia gracilis</i>
15	<i>Franseria deltoidea</i>	<i>Franseria deltoidea</i>	<i>Franseria deltoidea</i>
16	<i>Larrea tridentata</i>	<i>Franseria deltoidea</i>	<i>Krameria canescens</i>
17	<i>Franseria deltoidea</i>	<i>Franseria deltoidea</i>	<i>Franseria deltoidea</i>
A		<i>Larrea tridentata</i>	<i>Larrea tridentata</i>
B 1		<i>Larrea tridentata</i>	<i>Opuntia fulgida</i>
B 2		<i>Franseria deltoidea</i>	<i>Franseria deltoidea</i>
B 3		<i>Larrea tridentata</i>	<i>Larrea tridentata</i>
B 4		<i>Larrea tridentata</i>	<i>Opuntia leptocaulis</i>
B 5		<i>Larrea tridentata</i>	<i>Aplopappus hartwegi</i>
B 6		<i>Larrea tridentata</i>	<i>Aplopappus hartwegi</i>
B 7		<i>Krameria canescens</i>	<i>Krameria canescens</i>
B 8		<i>Larrea tridentata</i>	<i>Aplopappus hartwegi</i>

the last of these areas, on which it made no change. The one case in which a fresh species entered the areas was the invasion of *Aplopappus hartwegi*, which involved B 5, B 6 and B 8.

The most that can be said in regard to trends in the vegetational changes over such a short period as 30 years, is that the large perennials show small changes in number, the small woody perennials already present have increased greatly in numbers, the grasses have spread, and there has been some shifting of numerical dominance.

Examination of tables I to VII will show that the various observational areas differed in the physiognomy and composition of their vegetation in 1906. Although all of them are located within the same square mile, and S 15, S 16 and S 17 are separated by distances of 200 m. or less, there is nevertheless a substantial difference in their vegetational and floristic features. It will be noted also that there has been a marked difference between the areas with respect to the species that have increased during the period of protection. Also, the data for 1936 show that the diversity between the areas is fully as great as it was in 1906. The particular areas that have been under observation give, without doubt, only an incomplete picture of the continual change that is going on in the vegetation of the entire surrounding region. The lack of definite trends in the relatively small area that has been investigated is an indication of the highly sporadic character of vegetational change when studied over a short period, and a confirmation of our knowledge that these changes are controlled by a vast number of interacting conditions.

SUMMARY

On the grounds of the Desert Laboratory, at Tucson, Arizona, the perennial plants of 7 areas have been mapped and their changes followed for 30 years or less. Five areas 10 m. square were first mapped in 1906. One area of 557 sq. m. was enumerated in 1910, and one area of 800 sq. m. was mapped

in 1928. The laboratory grounds have been protected from grazing and other disturbance since 1907.

All of the areas established in 1906 have shown increases in plant population, which range from 42 per cent to 851 per cent. The increase in the last 8 years was greater than in the preceding 22 years, due to the slow and cumulative effect of the restoration of favorable conditions for establishment. The total number of large perennials has remained almost unchanged. Of the original large perennials 30 per cent died and were succeeded by nearly the same number of new individuals.

The increases of total plant population are due to newly established shrubs and bushes, particularly *Franseria deltoidea*, *Encelia farinosa*, *Caliandra eriophylla*, *Janusia gracilis* and *Coldenia canescens*. Grasses were a negligible component of the vegetation in 1906 but now cover 2.7 per cent of the 500 sq. m. comprised in the oldest areas.

The area of 800 sq. m. first mapped in 1928 has increased in plant population from 163 to 466, but 197 of the 303 new plants are young individuals of the range weed *Aplopappus hartwegi*.

The data secured in the enumerations give some indication of the length of life of the plants involved.

The diversity which characterized the vegetation of the areas at the outset has been perpetuated in the nature of the changes they have undergone and in the present composition of the vegetation of the several areas.

On the five oldest areas the number of species represented has decreased slightly on two and increased from 29 to 44 on the other three.

There is no common trend discoverable in the history of the various areas other than their consistent increase in population.

TEMPERATURE AND MOISTURE PREFERENCES OF WIREWORMS

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INTRODUCTION

During a study of the biology of wireworms² it was observed that these subterranean larvae had fairly definite habits in relation to soil moisture and temperature. They avoided dry soil, and when kept in dry soil they soon died of desiccation. On the other hand, saturated soil caused almost complete discontinuance of activity and sometimes death. High temperatures caused increased activity and low temperatures resulted in dormancy, while extremes of either caused death.

To check these field observations and get definite information on the temperature and moisture preferences of wireworms, several series of experiments were conducted under controlled conditions in the laboratory.

TEMPERATURE PREFERENCES

According to McColloch and Hayes ('23), the seasonal movement of white grubs in the soil coincides with the spring and fall "overtun" of temperature. Fulton ('28) has shown that temperature affects the movements of both adults and larvae of elaterids. To test this further, a more elaborate temperature gradient than that used by Fulton was constructed.

The device consisted of a galvanized-iron container, 74 inches long, 13 inches wide, and 8 inches deep, surrounded by fiber-board insulation $\frac{3}{4}$ inch thick, and all enclosed in wood (fig. 1). The inner container had three compartments, one at each end 12 inches long (*A* and *B*) and the middle one 50 inches long. The middle compartment contained sand, in which were imbedded two strips of galvanized eaves troughs (*DD*). Compartment *A* was kept filled with ice and salt and compartment *B* with hot water. Heat was supplied from an electric-light bulb inside a galvanized-iron can (*C*), which was immersed in the water in compartment *B*. The heat was controlled with a thermostat. The sand was kept moist to increase its conductivity. The troughs were marked at 2-inch intervals, from 0 at the cold end to 50 at the

¹ The writer is indebted to M. W. Stone, A. F. Howland, and C. S. Guy, of the Alhambra, Calif., laboratory, for assistance in carrying on these experiments.

² The species used was *Limonius (Phelates) californicus* Mann. (Coleoptera, Elateridae).

hot end, and at each interval a thermometer was inserted through a hole in the cover.

In conducting an experiment, the troughs were filled with sandy-loam soil, the apparatus was closed, and time was allowed for adjustment of the gradient of temperatures. By keeping the ice and salt mixture at slightly below freezing by repacking night and morning, and the hot water at 110° F., a gradient of 34° to 107°, inclusive,³ with slight variations in different experiments, was maintained inside the troughs. Temperatures between every 2 inches of soil differed from 1 to 8 degrees between points 0 and 10 inches and between points 40 and 50 inches, and from 1 to 3 degrees between 10 and 40 inches, the greater variations being near the ends.

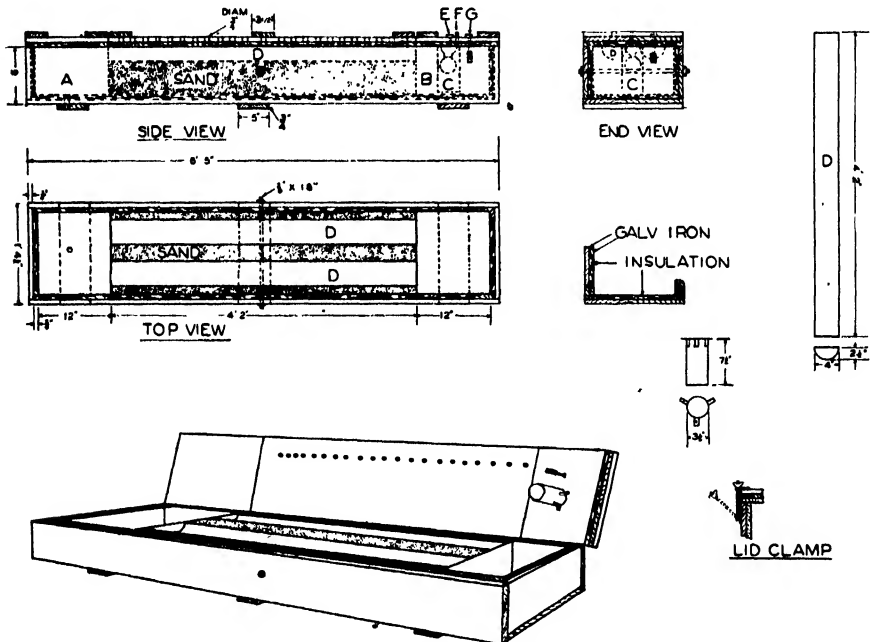


FIG. 1. Temperature gradient, showing construction details.

Wireworms were then placed in the soil in the troughs, and the apparatus was left undisturbed for several days. At the end of this time the temperatures for every 2 inches in the troughs were recorded. Then the soil was carefully sifted, 2 inches at a time, and the number of wireworms noted for the corresponding temperatures. Table I shows five typical gradient readings taken in the course of these experiments, and also the distribution of the wireworms in the gradient.

Two other gradients had been tried out, with the troughs and center compartment 36 and 60 inches long. In the shorter one the temperature varia-

³ All such groups mentioned hereafter are inclusive.

TABLE I. *Typical temperature readings and wireworm distribution*⁴ *in the 50-inch gradient.*
 One wireworm placed every 2 inches from 10 to 48

Inches.....	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50
October 20, 1930 Temperature, °F..... Wireworms found.....	44 {	48	53	55	57	59	61	63	64	65	67	68	70	71	72	74	76	77	79	81	83	85	89	92	98	106
April 28, 1931 Temperature, °F..... Wireworms found.....	43 {	47	51	54	56	58	60	61	62	64	65	67	68	69	70	71	73	74	76	78	80	82	85	88	94	99
May 19, 1931 Temperature, °F..... Wireworms found.....	38 {	41	47	50	52	54	55	57	59	60	61	62	63	64	66	67	69	70	72	74	76	78	81	85	91	97
May 22, 1931 Temperature, °F..... Wireworms found.....	39 {	44	48	51	54	56	58	59	61	61	62	63	64	65	67	68	70	71	73	75	77	79	83	88	92	100
May 13, 1931 Temperature, °F..... Wireworms found.....	47 {	49	51	53	55	58	59	61	62	63	64	65	66	67	69	70	71	73	74	77	79	81	86	90	95	102

⁴ In first four experiments the readings were taken 3 days, and in the last experiment 5 days, after the wireworms had been placed in the gradient.

tions every 2 inches were too great, while in the longer one there were several repetitions of the same temperature. The gradient with the 50-inch trough proved the most satisfactory and was used in all experiments recorded herein, except as noted.

In the experiments with the 60-inch gradient 20 wireworms were placed 2 inches apart from points 20 to 58, where the temperatures averaged 63° and 95° F. In the 50-inch gradient the wireworms were first distributed from 10 to 48, where the temperatures averaged 61° and 100°. Several times wireworms were also placed in the cold end, at temperatures from 36° to 40°, but this was apparently too cold, for they did not move at all. Then, to concentrate the wireworms a little more in the hot end, they were placed 1 inch apart from 30 to 49, where the temperatures ranged from 71° to 101°; in this case the worms quickly moved from the hot end. In an endeavor to place all the wireworms in an environment of more nearly equal temperatures, for the final experiments they were all placed from 44 to 46 inches, where the temperature range was 84° to 95°.

Although most of the wireworms placed in the hot end of the trough quickly moved to cooler soil, a few were able to persist above 90° F. It is believed that those remaining in the hot end were inactive because of an approaching molt. Occasionally a molt occurred in the hot end, but molting individuals were not counted.

In explaining his term "preferendum," Uvarov ('31) shows that insects will choose certain temperatures. This is not a strictly defined point, but a fairly wide zone. It was decided that the somewhat concentrated interval in which 50 per cent or more of the wireworms were found could logically be called "the preferendum," and this zone was accordingly ascertained. Its width in the soil gradient was found to be from 8 to 14 Fahrenheit degrees. For further analysis of the results, the entire temperature range was arbitrarily divided into 5-degree groups, and the one having the most wireworms determined. Also, the temperature at which the largest number of wireworms was found, the mode, was noted.

Several series of experiments were carried on at different times in the year. As these progressed it began to appear that the activities of the wireworms varied somewhat with the season. Accordingly the data have been grouped on a seasonal basis, and are summarized in table II and figure 2.

It was known, from field observations before the experiments were begun, that wireworms' activities are greatest in the spring and fall, continue throughout the summer where food is present and moisture is favorable, and decline to a minimum during the winter. In southern California their activity never ceases entirely.

The data for the first four series of experiments show that the temperature preferences change with the seasons, being low early in the spring, rising gradually throughout the summer to a peak early in the fall, and dropping again late in the fall and in the winter. Apparently during the winter the

TABLE II. *Summary of temperature preferences of wireworms, as shown by their distribution in the soil gradient, for different times of the year*

Date	Original distribution	Temperature range of original distribution	Temperature range of final distribution	Mode	5-Degree zone	Preferendum	Experiments
	<i>Inches</i>	<i>°F.</i>	<i>°F.</i>	<i>°F.</i>	<i>°F.</i>	<i>°F.</i>	<i>Number</i>
April 28 to May 25, 1931...	10-48	61-100	41-90	65	61-65	59-69	12
June 11 to July 5, 1930...	20-58 ^a	63-95	47-90	68	66-70	62-72	8
June 8 to Aug. 4, 1931...	10-48	62-96	60-95	75	71-75	66-76	10
Sept. 1 to 25, 1932...	30-49 ^b	71-101	42-100	80	76-80	73-82	16
Sept. 24 to Oct. 17, 1929...	20-58 ^b	62-103	41-94	70	66-70	64-71	8
Sept. 24 to Oct. 10, 1929...	2-40 ^b	41-73	41-83	66	61-65	60-67	6
Feb. 3 to Mar. 5, 1934...	44-46	84-95	45-99 ^c 46-94 ^d	65 63	61-65 66-70	62-74 56-69	10 10

^a In the 60-inch gradient; all other experiments in the 50-inch gradient.

^b One wireworm placed every inch between these points.

^c Wireworms confined at 80° F. for 2 weeks prior to experiment.

^d Wireworms confined at 48° F. for 2 weeks prior to experiment.

wireworms become accustomed to a lower temperature and the preferendum is found to be low. As the season advances and the soil warms up, the wireworms become adapted to the higher temperatures prevailing and their preferendum consequently is higher. There is a difference of 13 to 17 degrees in this preferendum between early spring and early fall. A similar difference is shown in the mode and in the 5-degree zone.

At Alhambra the monthly mean soil temperature is usually lowest in January, gradually rises to its highest point in July, and then declines, although occasionally December has the lowest temperature and August the highest.

In February 1934 wireworms were confined for 2 weeks without food in a constant-temperature cabinet, half at 80° F. and half at 48°, before being placed in the gradient troughs. The data for these experiments are summarized in table II and figure 2. The results confirm those of the previous experiments in a general way, with less difference than had been anticipated. It is observed that with the wireworms held at 48° the modes and the preferendum are somewhat lower than with the wireworms held at 80°, but the 5-degree zone is higher, which is contrary to expectations. There were a few more worms between 46° and 60° among those that were held at 48° than among those held at 80°. It is believed that the difference would have been greater if the period of confinement in the constant-temperature cabinets had been longer.

For additional information on the subject, old notes were examined, and two experiments conducted in September and October 1929 on the 60-inch gradient were found. These data are also summarized in table II and figure 2. When the wireworms were placed in the cold end of the gradient

(41° to 73° F.), the mode, the 5-degree zone, and the preferendum were 4 to 5 degrees lower than when placed at the warm end (62° to 103° F.).

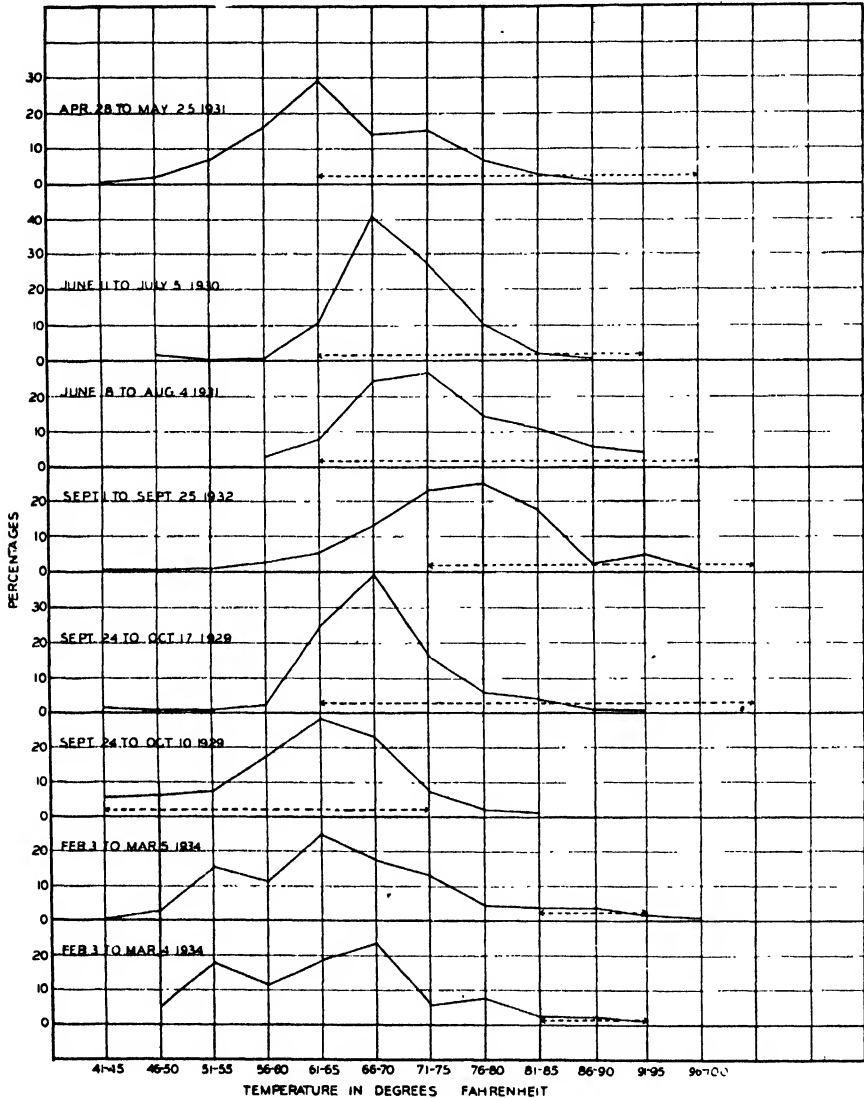


FIG. 2. Distribution of wireworms in the soil-temperature gradient, grouped in 5-degree zones. Continuous line, final distribution; broken line, original distribution.

A comparison of all the data, as summarized in table II, shows that the mode was lowest in the periods February 3 to March 5 and April 28 to May 25, or following the low temperatures of winter. During the summer

the mode rose until the high point (80° F.) was reached in September and then dropped in the latter part of September and October. The variation in the original distribution of the wireworms may have affected the results somewhat, but the fact that in February the wireworms were placed near the hot end of the gradient indicated that the season of the year had a greater influence. The distribution in the 5-degree zones and the preferendum showed a similar seasonal trend.

MOISTURE RELATIONSHIPS

To test the reactions of wireworms to soil moisture, a moisture-gradient apparatus (fig. 3) was made. It consisted of six galvanized-iron cylindrical

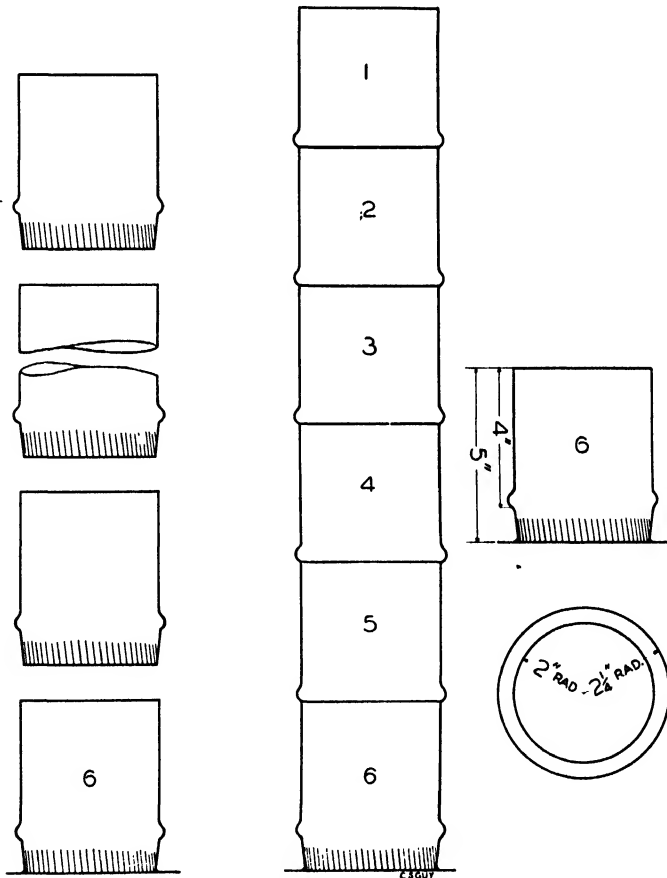


FIG. 3. Galvanized-iron moisture gradient, showing construction details.

sections, each 4 inches in diameter and 5 inches long, crimped at one end so they could be fitted together to make a continuous tube 24 inches long. To

the bottom of the lowest section was soldered a flat piece of galvanized iron, making a base upon which the entire tube could stand. Sun-dried, sifted sandy-loam soil was further dried in an oven at 130° F. for at least 2 days, and then sufficient water was added to give the desired percentage of moisture by weight. The bottom section (no. 6) was filled with soil containing 24 per cent of moisture, the next section (no. 5) contained 4 per cent less, and so on up to the top section (no. 1) which contained 4 per cent. For use in check experiments similar tubes were filled with soil of uniform moisture content, which ranged between 12 and 15 per cent in different experiments.

In the first set of experiments (series *A*) all the wireworms were introduced into the top section (no. 1), while the tube stood upright. After 4 days, which preliminary experiments had shown was sufficient time for the wireworms to become distributed, the tubes were taken apart and the number of wireworms in each section was recorded.

To determine if the search for food affected the migrations of the wireworms in the soil-moisture gradient, the experiments were repeated as described above, except that several kernels of wheat were placed in each section (series *B*).

TABLE III. *Location of wireworms in soil-moisture gradient after 4 days, Series A-E*

Series	Section in which wireworms were placed	Food	Position of tube	Number of experiments	Number of wireworms	Percentage of wireworms found in section ^a					
						1	2	3	4	5	6
A	1	No	Perpendicular	9	140	3.5	14.8	35.6	28.7	17.4	0
B	1	Yes	"	5	100	10.2	35.2	32.9	17.0	4.5	0
C	1	Yes	"	18	432	8.5	20.8	26.2	28.9	13.5	2.0
D	Each	Yes	"	8	240	4.5	8.5	12.9	32.1	23.7	18.3
E	1	Yes	Horizontal	19	456	7.7	27.9	24.2	24.4	12.1	3.7
Checks											
A	1	No	Perpendicular	4	70	40.6	24.6	10.1	11.6	11.6	1.4
B	1	Yes	"	2	30	48.2	13.8	24.1	6.9	6.9	0.0
C	1	Yes	"	8	192	33.3	30.6	16.7	6.5	8.6	4.3
D	Each	Yes	"	4	120	8.5	16.1	19.5	16.9	21.2	17.8
E	1	Yes	Horizontal	9	216	41.1	24.9	13.9	9.1	8.1	3.3

^a The moisture content of the different sections was as follows: No. 1, 4 per cent; no. 2, 8 per cent; no. 3, 12 per cent; no. 4, 16 per cent; no. 5, 20 per cent; no. 6, 24 per cent.

The results are shown in table III. In both cases a large percentage of the wireworms migrated into soils of high moisture content. In the checks, where the soil moisture was uniform throughout the tube, the movement downward was much less. The presence of food apparently retarded this movement to some extent, for more larvae remained in the 4-per cent sections (no. 1) where there was food than where it was absent. Also, more wireworms moved into the lower sections of the tube that had no food.

Later these experiments were repeated on a somewhat larger scale (series *C*), with similar results.

In the next set of experiments (series *D*) five wireworms, with several kernels of wheat, were placed in the center of each section. About 75 per cent of the wireworms moved out of the 4 per cent section and about 50 per cent out of the 8 per cent section (no. 2). The largest number were found in the section containing 16 per cent of moisture (no. 4). In the checks 50 per cent moved out of the top section, but there was relatively little change in the other sections.

This movement out of the top section suggested the possibility that gravity might have some effect on the movement of the wireworms. To test this, another set of experiments (series *E*) was performed in which the tubes were set horizontally. Food was placed in each section, and all the wireworms were put in the 4 per cent section. Practically the same percentage of worms remained in the top section as when the tube was perpendicular (compare series *C*). More wireworms remained in the 8 per cent horizontal section than in the corresponding perpendicular one, but in the 12, 16, and 20 per cent sections a few more larvae were found where the tube was perpendicular. The figures indicate that the movement out of 4 per cent moisture was due primarily to unfavorable environment. When 8 per cent was reached, the soil was moist enough to be satisfactory.

In the checks of all the experiments except series *D* from 33 to 48 per cent of the wireworms remained in the top section, and the others were scattered throughout the remainder of the tube. This is in contrast to the 3.5 to 10.2 per cent which remained in the top section containing only 4 per cent of moisture.

For further evidence of the effect of gravity, the 4 per cent moisture section was placed in the center of a seven-section tube with 8, 12, and 16 per cent sections on each side. All the wireworms were placed in the 4 per cent section. One set of tubes was placed horizontal and another set perpendicular.

The results are shown in table IV. With the horizontal tubes there was considerable movement in both directions, although it was greater toward what would have been the base had the tubes been perpendicular. The only explanation for this is that the tubes stood vertical while being filled, and the worms may have started downward before the tubes were placed horizontal. In the perpendicular tubes there was a movement of only 5.1 per cent of the worms upward, while 85.5 per cent moved out of the dry section downward into the moister sections. In the horizontal checks, with uniform moisture throughout the tube, 34.7 per cent of the worms moved toward the top end and 16.8 per cent toward the bottom end, whereas in the perpendicular checks only 14.9 per cent moved toward the top and 47.9 per cent toward the bottom.

TABLE IV. *Location of wireworms in soil-moisture gradient after 4 days, when wireworms were placed in center of 7-section gradient, and food was placed in all sections. Series F and G*

Series	Position of tube	Number of experiments	Number of wireworms used	Percentage of wireworms found in section ¹⁰						
				1	2	3	4	5	6	7
F	Horizontal	11	264	3.9	9.7	14.3	13.2	20.9	17.1	20.9
G	Perpendicular	12	288	—	1.1	4.0	9.5	19.3	26.2	40.0

Checks

F	Horizontal	4	96	4.2	9.5	21.0	48.4	12.6	3.2	1.0
G	Perpendicular	4	96	—	3.2	11.7	37.2	14.9	21.3	11.7

¹⁰ The moisture content of the different sections was as follows: no. 1, 16 per cent; no. 2, 12 per cent; no. 3, 8 per cent; no. 4, 4 per cent; no. 5, 8 per cent; no. 6, 12 per cent; no. 7, 16 per cent.

As a final test, the experiments were repeated with tubes containing sections of soil of 3, 6, 9, 12, 16, and 18 per cent moisture. The results, as shown in table V, confirm those previously obtained.

TABLE V. *Location of wireworms in soil-moisture gradient after 4 days, when food was supplied and wireworms were placed in top section, and the tube was kept perpendicular*

Tube	Number of experiments	Number of wireworms used	Percentage of wireworms found in section ¹¹					
			1	2	3	4	5	6
Gradient ¹¹	11	264	3.1	20.3	29.2	23.0	19.0	5.3
Check	4	96	47.9	14.9	15.9	9.6	6.4	5.3

¹¹ The moisture content of the different sections was as follows: no. 1, 3 per cent; no. 2, 6 per cent; no. 3, 9 per cent; no. 4, 12 per cent; no. 5, 15 per cent; no. 6, 18 per cent.

Throughout the investigation an occasional dead wireworm was found. The adverse effect of the dry soil was further shown by the fact that 90 per cent of the dead wireworms were found in the top section. Where the larvae were placed in each section, the 24 per cent moisture also caused some fatalities.

SUMMARY

A study has been made of the temperatures and moisture content of soil which are preferred by wireworms. The experiments show that the temperature preferendum varies with the season, being higher in the summer and fall than in the winter and spring. There is also a lag behind the soil temperature, indicating that the preferendum does not change until the wireworms have been subjected to the higher or lower temperatures for a month or more. In low temperatures wireworms become inactive, but high tem-

peratures are also unfavorable, the wireworms quickly moving to a more favorable environment. Finally, there is a rather wide range of temperature in which wireworms are active.

These experiments also indicate that, while dry soil has the greatest effect in causing the wireworms to move to a more favorable environment, the force of gravity exerts some influence, and when the wireworms are stimulated to activity by an unfavorable, dry environment, the natural trend of movement is downward.

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EFFECTS OF THE 1934 DROUGHT ON NATIVE VEGETATION OF THE UPPER SNAKE RIVER PLAINS, IDAHO ¹

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Through its deteriorating influence on both the quantity and the character of the forage, drought brings about severe overgrazing of already fully stocked ranges. Drought alone and in combination with overgrazing causes depletion in the plant cover and allows wind and water erosion to be accelerated. Because the cumulative results of drought are not easily apparent until they have progressed to an advanced stage, superficial recovery often prevents the casual observer from seeing the real facts.

Since modification of the drought itself is impossible, management of the range must provide for moderate forage use during extremely dry years. Forage production during "good" years does not necessarily build up a reserve to tide over subsequent drought years. Only in certain regions do grasses, unutilized in previous years, afford protection against starvation losses among livestock without severe overgrazing of the more palatable current production.

In many cases, damage from overgrazing current plant growth in years of low forage production offsets the results of several years of wise management. Forsling ('34) states that failure to get favorable responses during good years is often the result of a change in character of vegetation following intensive grazing. Range deterioration from overgrazing in a drought year is rarely made up in the normal years that follow. One drought lowers production to a level that usually persists until it is still further depressed by another year of deficient rainfall.

EFFECTS OF 1934 DROUGHT

One of the most severe and extensive droughts in the history of the west occurred in 1934. Widespread interest as to the effects of this drought on native vegetation has brought out many conflicting opinions, some with but little factual basis. Beath ('35) reported that on the Red Desert of Wyoming only grasses were damaged. Wheatgrasses (*Agropyron* spp.) suffered the least, while ricegrasses (*Oryzopsis* spp.) and junegrasses (*Koeleria* spp.) suffered the most injury. An anonymous writer ('35) states that ranges estimated in 1934 to be 50 to 75 per cent dead carried in 1935 the most luxuriant grass in years. In Colorado, Allred ('35) quotes McConnell as

¹ A study conducted in cooperation with the Bureau of Animal Industry, U. S. Department of Agriculture, at the U. S. Sheep Experiment Station, Dubois, Idaho.

finding in 1935 a 40 per cent kill among the more palatable grasses but that losses were veiled by a temporary profusion of annual plants. Weaver et al. ('35) found on upland species of the tallgrass prairie of eastern Nebraska that early maturity and a decreased total height resulted from the 1934 drought.

In order that the magnitude and character of changes brought by severe recurrent drought periods may be more fully realized, the results of 4 years' detailed study from 1932 to 1935 at the U. S. Sheep Experiment Station, Dubois, Idaho, are here presented.

DESCRIPTION OF THE RANGE AREA

Ranges at the U. S. Sheep Experiment Station in the upper Snake River plains in Clark County, Idaho, are broadly representative of large areas of sagebrush-wheatgrass ranges in the southern part of that state. The semi-arid climate is characterized by wide diurnal and annual variations in temperature and by erratic precipitation. Soil moisture most effective in plant growth is ordinarily obtained from winter snow and from spring and early summer rains. The soil is a thin mantle of fine basaltic, sandy loam with frequent exposed reefs of basalt.

The most conspicuous components of the vegetation are the fine-leaved threetip sagebrush, *Artemisia tripartita*, big sagebrush, *Artemisia tridentata*, horsebrush, *Tetradymia canescens incrimis*, bitterbrush, *Purshia tridentata*, and rabbitbrush, *Chrysothamnus puberulus*. Beneath the shrubs are grasses and weeds, which are less abundant but nevertheless furnish most of the forage. The grass species, listed in order of abundance, are as follows: Bluebunch wheatgrass, *Agropyron spicatum*, needle-and-thread, *Stipa comata*, Indian ricegrass, *Oryzopsis hymenoides*. Sandberg bluegrass, *Poa secunda*, Nevada bluegrass, *Poa nevadensis*, and thickspike wheatgrass, *Agropyron dasy-stachyum*. Characteristic also are the following herb species: balsamroot, *Balsamorhiza sagittata*, hawksbeard, *Crepis acuminata*, lupine, *Lupinus caudatus*, and mountain dandelion, *Agoseris taraxacifolia*.

METHODS OF STUDY

Four enclosures with areas of 80, 10, 0.5 and 0.5 acres respectively, were used to determine the effect of climate on ungrazed vegetation. In these four areas are located 18 meter quadrats and 140 permanent sample plots. Quadrats were mapped annually with a pantograph (Pearse et al, '35). Permanent circular sample plots of 100 square feet area and located at mechanical intervals were estimated annually. Ten plants each of five important grasses (*Agropyron spicatum*, *Stipa comata*, *Oryzopsis hymenoides*, *Poa secunda* and *Poa nevadensis*) and three important weed species (*Balsamorhiza sagittata*, *Crepis acuminata* and *Lupinus caudatus*) were measured and observed at 5-day intervals from the date snow disappeared until herbage was cured in midsummer.

Continuous temperature and precipitation records were afforded by the cooperative weather station on the grounds.

Statistical analysis

Significance of changes between years was tested by using Fisher's "t" test. Odds of 19 to 1 are considered significant, those of 99 to 1 very significant.

Average trend of climate and of vegetation responses

Normally, all growth is completed and in many years herbage has cured prior to July. Fluctuations in climate after July 1 affect vegetative growth to an important degree only in the following year. Therefore, all compilations are based on a vegetational year ending June 30 and divided into three periods: (1) summer—July, August and September; (2) winter—October to March inclusive; and (3) spring—April, May and June.

The majority of plant species, usually in a semidormant state, seem unable to take important advantage of any moisture replenishment in the surface soil afforded by the normal summer precipitation (2.60 in.)

Soil-moisture reserves for the subsequent spring growing season are built up from late fall rains and from accumulated winter snowfall. Though precipitation is light, plant growth depends largely upon the 4.11 inches of moisture which normally falls during the winter period.

Growth generally begins by April 1 and plant functions are largely completed by July 1, except in the cases of *Artemisia tridentata*, *Artemisia tripartita*, *Chrysothamnus* spp., and a few of the herbaceous perennial composites and annuals that flower in late summer. Precipitation during May and June, normally the heaviest of the entire year, supplements the soil moisture stored during the winter. Frequently, however, slow growth, owing to low temperatures in early spring, allows high winds to evaporate much soil moisture.

CLIMATE OF THE PERIOD 1932-1935

Meteorological records, continuous only since 1924, are indicative of the position that the period 1932 to 1935, inclusive, occupies with reference to past climate at the U. S. Sheep Experiment Station. Weather records at Idaho Falls, 50 miles south, since 1881 show a normal yearly precipitation of 11.51 inches with a virtually unbroken dry period starting in 1918. Since the precipitation curves for the past 11 years at the U. S. Sheep Experiment Station and at Idaho Falls are reasonably comparable, it is safe to conclude that precipitation at the Sheep Station has been subnormal since 1918 and that 1934 was preceded by a dry period of 14 years' duration.

Meteorological records at the U. S. Sheep Experiment Station show a mean annual precipitation of 9.79 inches (table I).

Records for the years 1931-32 and 1932-33 show positive departures from this mean of 0.80 inch and 1.05 inches respectively, while data for 1933-34 and 1934-35 show deficiencies of 2.52 and 1.28 inches. The driest year on

TABLE I. *Precipitation and mean monthly temperatures 1931-32, 1932-33, 1933-34, 1934-35, and average 1925-1935*

	Precipitation, inches					Temperature, degrees F.				
	11-year aver.	1931- 32	1932- 33	1933- 34	1934- 35	11-year aver.	1931- 32	1932- 33	1933- 34	1934- 35
Annual	9.79	10.59	10.84	7.27	8.51	47.5	45.4	44.2	53.2	48.1
July	.63	.67	2.52	.06	.00	69.5	73.3	66.4	72.8	72.5
August	.99	.68	1.29	1.04	.06	66.4	68.9	66.6	66.1	71.6
September	.98	.82	.02	.52	.41	55.1	57.9	58.6	56.5	53.4
Summer	2.60	2.17	3.83	1.62	.47	63.7	66.7	63.8	65.1	65.8
October	.89	.14	.27	.36	1.49	44.6	46.7	40.7	49.6	50.0
November	.73	.69	.36	.35	1.51	31.6	27.8	33.5	34.0	34.8
December	.83	2.46	.47	.87	.70	20.6	20.0	13.5	28.1	23.0
January	.62	.70	1.91	.55	.54	21.6	11.8	17.0	26.6	21.8
February	.58	.55	.41	.36	.29	25.9	18.6	9.8	34.2	24.1
March	.46	.23	.31	.15	.87	31.5	24.0	28.8	44.7	28.6
Winter	4.11	4.77	3.73	2.64	5.40	29.3	24.8	23.9	36.2	30.4
April	.87	.87	.92	.34	1.80	42.9	40.2	40.0	51.6	40.0
May	1.10	.74	2.10	.42	.78	52.4	51.9	46.6	60.8	48.6
June	1.11	2.04	.26	2.25	.06	60.1	58.4	65.1	60.2	60.6
Spring	3.08	3.65	3.28	3.01	2.64	51.8	50.2	50.6	57.5	49.7

record, 1933-1934, was more deficient by 0.85 inch than was 1928, the next driest (fig. 1). With a precipitation of 8.51 inches, 1934-35 was the third driest year on record. The three years 1927, 1928, and 1930 were subnormal in precipitation.

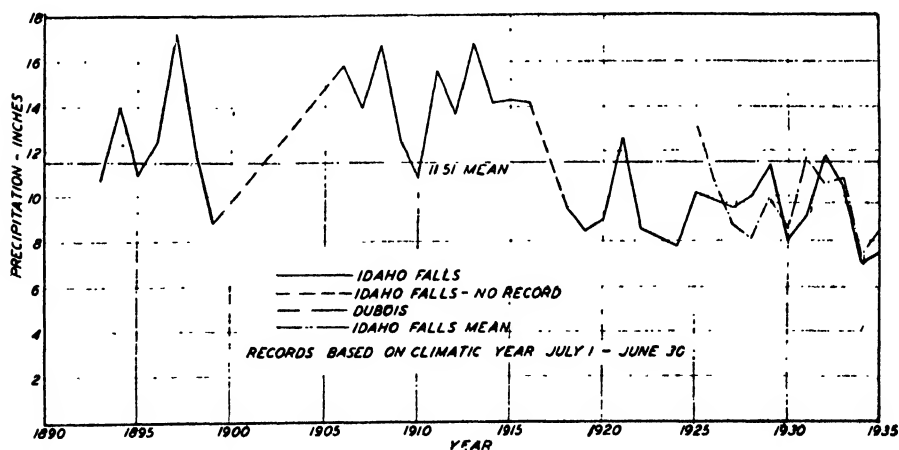


FIG. 1. Precipitation at Idaho Falls for 1882-1935 and at Dubois for 1925-1935.

With excellent winter precipitation coming largely in December, 1932 (2.46 in.), soil moisture was sufficient in 1933 to keep the plants growing until the time of early June rains. Extraordinary precipitation of 2.52 inches in July and 1.29 inches in August kept grasses growing actively throughout the summer. Snowfall for the winter of 1932-33, except for January, was below average. Spring precipitation in 1933 and late summer rains in 1932 were sufficient to maintain an average vegetative growth in 1933.

The drought of 1933-34 was broken only by slightly above average precipitation in August and December. At the inception of growth on March 1 a precipitation deficiency of 2.14 inches had accumulated, and by June 1 had increased to 3.66 inches. A series of storms beginning on June 6 brought a total of 2.25 inches for that month.

The summer of 1934 was the driest on record. July had no precipitation; August .06 inch and September .41 inch. Fall rains totaling 1.49 inches in October and 1.51 inches in November, both figures substantially above average, brought an otherwise unfavorable winter precipitation to 5.40 inches or 31 per cent above average. April (1935) precipitation of 1.80 inches brought the combined winter and spring moisture to slightly above average despite the drought in May and June.

Drought periods generally were accentuated by high temperatures and by strong dry winds; whereas the years 1931-32 and 1932-33, with highly favorable moisture, conformed very closely to average temperatures. Beginning with September 1933, temperatures were consistently above average, allowing high evaporation which further augmented the deficiency of the winter precipitation. Mean monthly temperatures, above average by 8.3° F. in February and 13.2° in March, incited plant growth about March 1, 1934, a month ahead of normal. Temperatures continued high throughout April and May but the abundant precipitation in June cooled off the weather almost to average.

The vegetational year 1934-1935 was rather warmer than normal except that low temperatures prevailed during March, April and May when moisture was abundant.

RESPONSES OF NATIVE VEGETATION TO CLIMATIC CONDITIONS

Three sources of information as to the trend of vegetational response are available for study: (1) data from the plant-development series indicate the rate of seasonal plant development and growth; (2) data from quadrats present basal area of plants and the number of plants by species; (3) data from estimation plots show the density of the plant cover, *i.e.* the percentage of the ground area covered by plant growth.

Seasonal development and growth

Data on seasonal development and growth from two species, *Agropyron spicatum* and *Balsamorhiza sagittata*, are presented as reactions typical of

grasses and herbs. When development and rapidity of growth in 1932 and 1933 are used as a basis, the extreme abnormality of 1934 is immediately apparent (fig. 2). In that year growth of *Agropyron spicatum* began about March 1. Owing to high temperatures, and a seasonal precipitation which was 35 per cent below normal at the beginning of the growing season, plant growth discontinued by the first of May when at a height of only 60 per cent of the 1932-1933 growth (table II). The few flower stalks produced were

TABLE II. *Summary of height growth and flower stalk production, plant development series (1932-1935)*

	1932	1933	1934	1935
<i>Agropyron spicatum</i> , leaf height, cm.	19.6	19.1	11.6	20.1
Per cent producing flowerstalks	60	100	10	100
Flower stalks per plant	*	7.6	0.1	22.3
<i>Balsamorhiza sagittata</i> , leaf height, cm.	25.4	25.6	15.9	23.6
Per cent producing flowerstalks	50	0	40	100
Flower stalks per plant	1.5	0	2.3	9.8

* No record.

ripened prematurely by hot dry winds. *Balsamorhiza sagittata* started growth March 25, a month early, and discontinued by May 1 after attaining a height of only 60 per cent of average. This was the only herb that produced flower stalks that year, few of which matured seed. By June 1, nearly all herbaceous vegetation had cured and some species, especially herbs, seemed to be exterminated. The 2.25 inches of precipitation in June came too late to be of material aid in herbage production, and 1934 plant growth was reduced even more than might have been expected, judging from the total yearly precipitation.

Fall rains in October and November were sufficient in intensity to start regrowth of grass, principally of *Poa* spp., *Agropyron spicatum*, and *Koeleria cristata*. This aftermath remained green throughout the entire winter and in March and April of 1935 these plants apparently resumed photosynthesis for about a month before drying.

Checked by low spring temperatures, plants in 1935 were unable to make the best use of an abundant supply of soil moisture. Despite unfavorable temperatures, however, the vegetation responded to increased precipitation. By June 1 height growth was average and flower production surpassed all previous records, presenting a picture of apparently complete recovery of all plants despite the injuries of 1934.

Agropyron spicatum, *Stipa comata*, and *Oryzopsis hymenoides*, which normally produced abundant leafage, were masses of flower stalks with little vegetative growth. In other respects, seasonal development and growth in 1935 were comparable to that in 1932 and 1933 (fig. 2 and table II). There was an excellent seed crop in 1935 (fig. 3).

Height growth of grass, taken as indicative of vigor, conveys the impression that effects of the 1934 drought had not been severe upon surviving plants. This situation is probable as long as protracted drought has not ma-

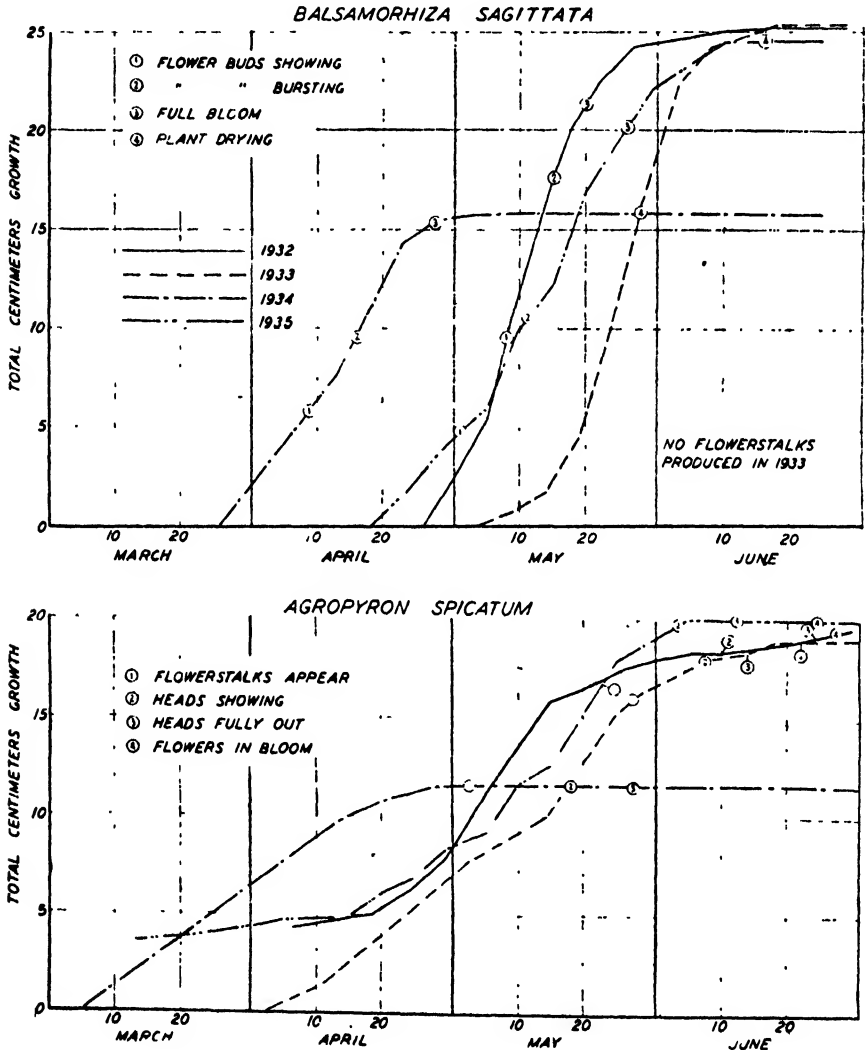


FIG. 2. Basal leaf growth and seasonal development.

terially decreased the extent of the live root system. As McCarty ('35) and Sampson and McCarty point out, most of the plant yield is the product of foods manufactured currently, and stored food is largely effective only in the inception of spring growth. That height growth in 1935 equalled that

of 1932 and 1933 seems to indicate that root systems of surviving plants had not been seriously injured in the 1934 drought.

Basal area and number of plants

Data regarding the effects of the 1934 drought on the basal area and on the number of grasses and herbs are shown in tables III and IV. Grasses

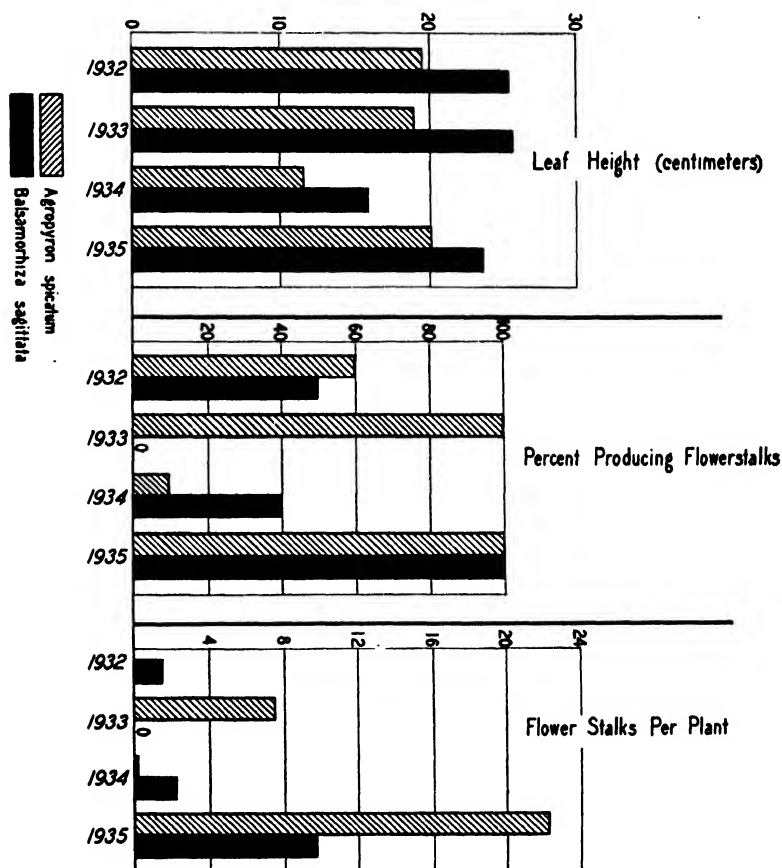


FIG. 3. Effects on *Agropyron spicatum* and *Balsamorhiza sagittata* of partial drought in 1933 and severe drought in 1934 on leaf height, percentage of plants producing flower stalks, and the number of flower stalks per plant in comparison with the approximately normal year of 1932. Recovery after the drought is shown for 1935, another fairly normal year.

show an increase in 11 sq. cm. from 1932 to 1933; a decrease of 232 sq. cm. in 1934, and a continued decline in 1935. Statistically, only the sharp drop in 1934 is significant. Though the basal area of plants decreased, the number of grass clumps consistently increased throughout the entire period.

TABLE III. Summary of trend of average basal area (in sq. cm.) and numbers of plants per meter-square quadrat 1932-1935

Species		1932	1933	1934	1935
<i>Agropyron spicatum</i>	Area	295	321	187	181
	No.	41.4	57.6	65.1	58.1
<i>Stipa comata</i>	Area	121	124	77	69
	No.	5.2	12.4	14.4	17.8
All grasses	Area	559	570	338	337
	No.	76.3	117.4	117.6	124.9
Perennial herbs	Area	18	138	78	121
	No.	42.6	44.8	26.4	48.2
Annual herbs	No.	58.2	12.7	0	120.1

TABLE IV. Significance of differences in basal area (in sq. cm.) and numbers of plants between years during the period 1932 to 1935

Species		1932-1933		1933-1934		1934-1935	
		Diff.	Fisher's "t"	Diff.	Fisher's "t"	Diff.	Fisher's "t"
<i>Agropyron spicatum</i>	Area	+26	1.25	-134	6.19 ²	-6	.26
	No.	+16.2	3.89 ²	+7.5	1.36	-7.0	2.94 ²
<i>Stipa comata</i>	Area	+3	.45	-47	2.99 ²	-8	1.01
	No.	+7.2	2.17 ¹	+2.0	.88	+3.4	.98
All grasses	Area	+11	.38	-232	10.04 ²	-1	.04
	No.	+41.1	5.41 ²	+0.2	.02	+7.3	1.23
Perennial herbs	Area	+120	3.57 ²	-60	3.28 ²	+43	4.46 ²
	No.	+2.2	4.68 ²	-18.4	1.81	+21.8	3.85 ²
Annual herbs	No.	-45.5	2.39 ¹	-12.7	1.21	+120.1	2.96 ²

¹ Exceeding 2.101—significant—odds of 19 to 1.² Exceeding 2.878—very significant—odds of 99 to 1.

Trends in *Agropyron spicatum* and *Stipa comata* largely indicate the trends for total grasses, since these two species comprise 74 per cent of the grass basal area and 74 per cent of the number of plants. *A. spicatum* and *S. comata* increased slightly in 1933; lost 42 and 38 per cent respectively of their 1933 areas in 1934, and continued to decrease in 1935. In numbers both species increased significantly in 1933. In 1934 a breaking up of individual clumps caused an additional increase in numbers. Having disintegrated badly in 1934, mortality of smaller individuals and clump remnants caused *A. spicatum* to decrease significantly in 1935. In contrast, *S. comata* clumps, with less injury in 1934, continued to disintegrate in 1935, thereby causing a sharp increase in numbers.

Figure 4, a map of a portion of one of the 18 quadrats, portrays the changes indicated in table III. The two major species were apparently so

severely affected in 1934 as to be incapable of immediate recovery, and except for the delayed "break-up" of *S. comata*, the reactions of the two species were similar.

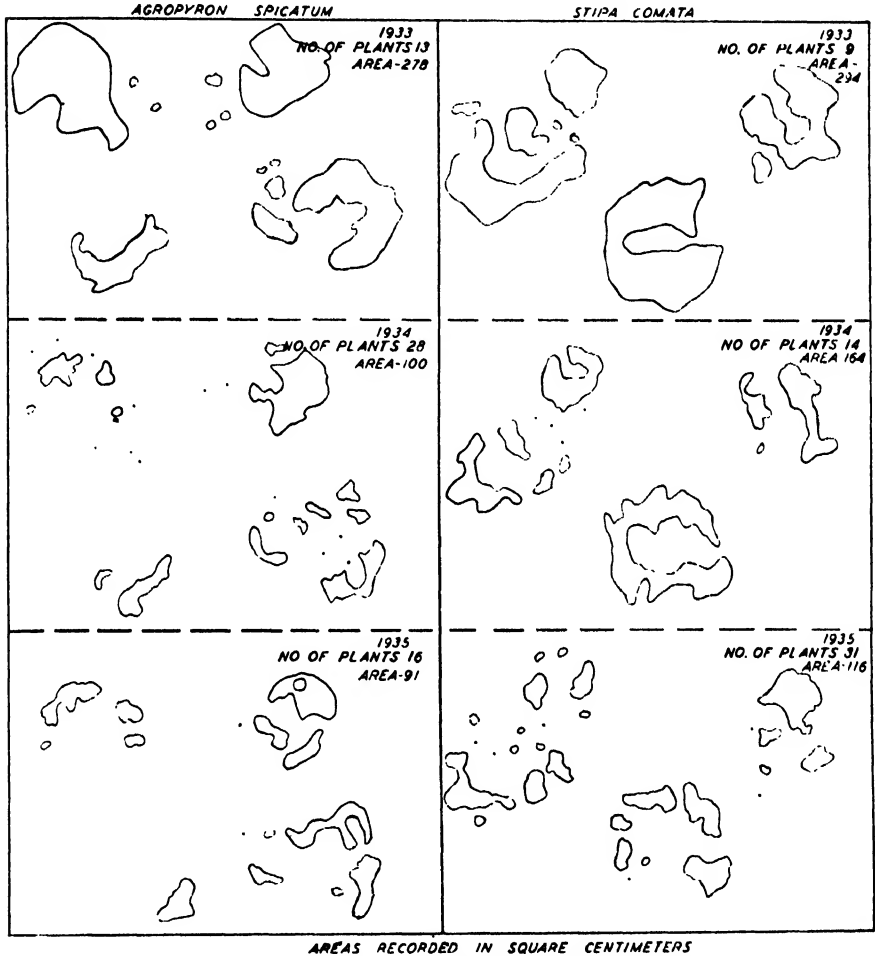


FIG. 4. Disintegration of large grass clumps on ungrazed quadrats for 1933-35.

Basal areas of perennial herbs are small in relation to aerial growth, and are not a reliable indicator of changes. The number of perennial herb plants shows slight increase in 1933; a 41 per cent decrease in 1934, and in 1935 a recovery to 122 per cent of the 1932-1933 average. In keeping with the favorableness of the season, the number of annual herbs fluctuates to a greater degree than does the number of perennials.

Effect of drought on grass clumps by size-class

Reactions of individual plants of *Stipa comata* and *Agropyron spicatum* have been traced from 1933. Individual plants were recorded in 1933 and changes in the individuals and in the clumps they produced were traced during 1934 and 1935. These have been grouped into size-classes and are presented

TABLE V. *Change by size-classes in grass area and numbers due to drought. Size-classes and areas in square centimeters*

Size-class	Area						Number of plants					
	1933		1934		1935		1933		1934		1935	
	Sq. cm.	%	Sq. cm.	%	Sq. cm.	%	No.	%	No.	%	No.	%
<i>Agropyron spicatum</i>												
0.5-10	1752	100	1001	57.1	982	56.0	875	100	730	83.4	554	63.3
11-30	1394	100	839	60.2	818	58.7	83	100	173	208.4	205	246.9
31-60	1285	100	685	53.3	619	48.2	37	100	99	267.5	123	332.4
61-	1546	100	793	51.3	698	45.1	30	100	128	461.0	171	650.0
<i>Stipa comata</i>												
0.5-10	266	100	166	62.2	160	60.0	152	100	152	100	140	92.1
11-30	485	100	306	63.0	334	68.7	24	100	35	145.8	42	175.0
31-60	428	100	266	62.1	244	57.0	10	100	17	170.0	26	260.0
61-	980	100	614	62.6	365	45.9	15	100	17	113.3	73	486.7

in table V. It will be seen that the changes in area of the two species are closely comparable. Decreases in the basal area in the drought year and in the following year are less in the smaller size-classes.

A. spicatum clumps disintegrated rapidly, the larger clumps breaking up to a greater extent than did the smaller ones. Individual small plants, however, pronouncedly decreased in numbers and continued to do so in 1935, more than offsetting the increase arising from disintegration of larger clumps. With *S. comata* the delay in disintegration of the larger clumps resulted in a slight increase in 1934 and a sharp increase in 1935.

The reactions are consistent in that each grass clump may be regarded as an aggregate of individual plants each one of which may develop into a clump by spreading intravaginal shoots. The clump is a family in which individual plants are held tightly together by a matrix of dead fibrous roots and shoots. The ultimate size of a clump in arid localities depends upon available moisture. As the diameter of the clump increases, individuals within the interior are least favorably located and under stress may succumb, forming a hollow-centered clump. The larger the clump size and the more nearly it is

in equilibrium with ordinary available moisture, the more severe are the effects of drought.

Clumps that are so badly disintegrated by drought or other causes that considerable basal area is lost, will no doubt increase more or less gradually with the return of more favorable conditions. Under arid conditions, the return to their former size will probably be slow, requiring as long a period as it would for a young clump to develop to a like size.

Density of vegetation

Plant density trends from 140 estimation plots are summarized in table VI, and the statistical significance of density changes are shown in table VII.

With the exception of *Balsamorhiza sagittata* and *Crepis acuminata*, all densities, as recorded in 1933, increased from 2 to 33 per cent. Since these two species constitute 72 per cent of the total herb density, herbs as a whole decreased significantly. As measured by "t" values, highly significant increases occurred in *Stipa comata*, in "other herbs" and in *Purshia tridentata*. "All grasses" showed an increase of 13.6 per cent and "all shrubs" an increase of 5.9 per cent, as a result of consistent increases in individual grass and shrub species. Increases were of such magnitude and were so consistent that they offset the 9.1 per cent decrease in herbs, and produced a significant 4.0 per cent increase in total vegetation.

TABLE VI. Trends in density of plant cover, 1932-1935, expressed in percentage of ground

Species	Average density				Per cent of 1932		
	1932	1933	1934	1935	1933	1934	1935
All vegetation	.16906	.17564	.06568	.14258	103.9	38.9	84.3
<i>Agropyron spicatum</i>	.03070	.03348	.01278	.01222	109.1	41.6	39.8
<i>Stipa comata</i>	.00051	.00205	.00106	.00072	100.0 ¹	51.7 ¹	35.1 ¹
Other grasses	.01121	.01267	.00228	.00737	113.0	20.3	65.7
All grasses	.04242	.04820	.01612	.02031	113.6	38.0	47.9
<i>Astragalus salinus</i>	.00195	.00198	—	.00098	101.5	0	50.3
<i>Balsamorhiza sagittata</i>	.02780	.02015	.00889	.04014	72.5	32.0	144.4
<i>Crepis acuminata</i>	.00424	.00420	.00040	.00430	99.1	9.4	101.4
Other herbs	.01080	.01440	.00194	.01207	133.3	18.0	111.8
All herbs	.04479	.04973	.01123	.05749	90.9	25.1	128.4
<i>Artemisia tripartita</i>	.05788	.05906	.02819	.04012	102.0	48.7	69.3
<i>Chrysothamnus puberulus</i>	.00824	.00922	.00240	.00845	111.9	29.1	102.5
<i>Purshia tridentata</i>	.00456	.00613	.00224	.00364	134.4	49.1	79.8
<i>Tetradymia canescens inermis</i>	.00979	.01090	.00478	.00974	111.3	48.8	99.5
All shrubs	.08186	.08670	.03834	.06298	105.9	46.8	76.9

¹ Computed using 1933 density as 100 per cent.

TABLE VII. *Differences in density of vegetation and significance of difference between successive years, 1932 to 1935. Density expressed as percentage of ground cover*

Species	1932-1933		1933-1934		1934-1935	
	Diff. density	Fisher's "t"	Diff. density	Fisher's "t"	Diff. density	Fisher's "t"
All vegetation	+ .00658	2.48 ¹	-.10996	30.58 ²	+ .07690	14.58 ²
<i>Agropyron spicatum</i>	+ .00278	2.50 ¹	-.02070	16.23 ²	- .00056	.45
<i>Stipa comata</i>	+ .00154	3.09 ²	-.00099	2.94 ²	- .00034	1.59
Other grasses	+ .00146	1.30	-.01039	12.43 ²	+ .00509	8.88 ²
All grasses	+ .00578	3.72 ²	-.03208	19.40 ²	+ .00419	5.79 ²
<i>Astragalus salinus</i>	+ .00003	1.18	-.00198	2.92 ²	+ .00098	3.42 ²
<i>Balsamorhiza sagittata</i>	- .00765	3.45 ²	-.01126	9.99 ²	+ .03125	10.52 ²
<i>Crepis acuminata</i>	- .00004	.12	-.00380	5.39 ²	+ .00390	7.29 ²
Other herbs	+ .00360	3.04 ²	-.01246	9.92 ²	+ .01013	10.43 ²
All herbs	- .00406	5.76 ²	-.02950	11.77 ²	+ .04626	12.70 ²
<i>Artemisia tripartita</i>	+ .00118	1.63	-.03087	24.38 ²	+ .01193	9.76 ²
<i>Chrysothamnus puberulus</i>	+ .00098	1.14	-.00682	8.09 ²	+ .00605	9.05 ²
<i>Purshia tridentata</i>	+ .00157	3.35 ²	-.00389	6.41 ²	+ .00140	4.61 ²
<i>Tetradymia canescens inermis</i>	+ .00111	1.66	-.00612	8.16 ²	+ .00496	7.34 ²
All shrubs	+ .00484	3.70 ²	-.04836	29.60 ²	+ .02464	11.92 ²

¹ Significant—odds of 19 to 1.² Very significant—odds of 99 to 1.

Severe decreases in density, all highly significant statistically, occurred in 1934 in all classes and species of plants when compared with 1932. Density of the herbs was reduced 74.9 per cent. Individual herb-species, which varied widely, decreased from 68.0 to 100 per cent of 1932, with *Balsamorhiza sagittata* decreasing the least of all. Grass densities were less severely affected, the decrease for all grass being 61.1 per cent. "Other grasses," principally of *Poa* spp. and *Koeleria cristata*, decreased almost 80 per cent. Shrub species were rather uniformly affected but less severely than either of the herbaceous groups, the decrease being 53.2 per cent. *Chrysothamnus puberulus*, nearly herbaceous in growth habit, suffered most severely.

In 1935 all vegetation increased from 38.9 per cent to 84.3 per cent of the 1932 density. With the exception of *Agropyron spicatum* and *Stipa comata*, which suffered losses additional to those of 1934, all species and groups of plants increased significantly. Even though other grass species increased sufficiently more than to offset the small losses in these two species, the 1935 grass density reached only 47.9 per cent of 1932. Herb species as a group seemed to have retained enough vigor that with the help of better moisture conditions in 1935, they increased to 128.4 per cent of 1932. Shrub species varied in their response to moisture, but as a whole, they did not regain their

1932 densities. The woody species *Artemisia tripartita* and *Purshia tridentata* returned to 69.3 and 79.8 per cent respectively; whereas, the more herbaceous *Chrysothamnus puberulus* and *Tetradymia canescens inermis* returned to 102.5 per cent and 99.5 per cent of their 1932 densities.

The ranges as a whole, superficially appeared to have recovered from the 1934 drought, because the great increase in perennial and annual herbs concealed the depleted condition of grasses.

DISCUSSION

Grasses were so seriously injured by the drought of 1934 that their condition, compared with that of 1932, showed a decrease in basal area of 60 per cent, in height of 60 per cent and in density of 38.9 per cent. Since density, or estimated ground cover, is a reflection of both basal area and height total density closely approximates their product. Although a small but significant increase of total grass density occurred in 1935, disintegration and death of grass clumps continued, resulting in small additional decreases in total basal area. As judged by height growth, those portions of grass clumps that survived the drought were not impaired in vigor since height of basal leaves in 1935 approximately equaled that of 1932. That protracted injury to the vigor of the grasses occurred, however, is shown by their density remaining at 47.9 per cent and their basal area at 60.0 per cent of 1932 figures. Individual grass species differed in their responses from the general behavior of "total grasses."

Two species, *Agropyron spicatum* and *Stipa comata*, forming 74 per cent of all grass basal area and density reacted similarly to other species in 1934, but did not respond favorably to better growing conditions in 1935. As a group, therefore, grasses continued to decrease in basal area and increased only slightly in density with the better conditions in 1935 despite the marked increases in minor species.

In 1934 perennial herbs, which as a group reacted more promptly to drought than either grasses or shrubs, decreased in number to 60 per cent of 1932. Annual weeds entirely disappeared. Basal leaf height of herbs decreased to 53 per cent of 1932 and density decreased to 25 per cent. Density loss in herbs, therefore, must have been caused by a combination of decreases in number, in height, and in leaf area.

Following favorable fall and spring precipitation, perennial herbs in 1935 so completely overcame the drastic reductions of 1934 that there were 5.6 more plants per meter quadrat than in 1932. Herb density increased to 28 per cent above the 1932 level and showed a recovery of 103 per cent from the 1934 level. The prolific production of 120 annual weeds per square meter is not markedly reflected in density because of the sparseness of foliage and diminutive size of these plants.

SPAWNING OF *VENUS MERCENARIA* (L.)¹

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INTRODUCTION

During recent years the spawning phenomena of pelecypod mollusks have been extensively studied by many investigators. As a result of these studies it became known that animals living in the water are subjected to several factors which either directly or indirectly affect their reproductive activities. Of these factors, temperature, chemical stimulation, abundance of food, and probably phases of the moon are of chief importance. Ordinarily, not the single but the combined influences of several factors control the sexual activities of mollusks.

The relation of spawning to water temperature has so far received more attention than the other relations. At present, on the basis of information contributed by numerous observers, it may be concluded that the influence of temperature upon the breeding of bivalve mollusks is of paramount importance. It has been shown by many workers that pelecypod mollusks breed at a definite temperature, which is constant for the species. In all forms studied, spawning occurs during rising temperatures of spring and summer. The critical spawning temperatures of different groups of bivalves vary greatly, extending from 5.0 to 30.0° C. (Nelson, '28a). Nelson states that the spawning temperature of *Mya arenaria* and *Mytilus edulis* is between 10–12° C. (50–54° F.). *Teredo navalis* spawns at the same temperature (Grave, '28). *Pecten irradians* begins to spawn at 15–16° C. (Belding, '10).

The genus *Ostrea* has received much more attention from investigators than any other allied form. The larviparous European oyster, *O. edulis*, breeds, according to Orton ('20), at a temperature of 59–61° F. (15–16.1° C.). The spawning habits of the American oyster, *O. virginica*, were studied by many investigators whose conclusions on the critical spawning temperature for this animal are quite similar, namely, that spawning begins when the temperature of the water reaches 68–70° F. (20–21.1° C.). *Ostrea gigas*, according to Amemiya ('29), requires a temperature of 25.0° C. to commence spawning, while *Ostrea cucullata* spawns when the water temperature reaches 26.7–30.6° C. (Awati and Rai, '31).

The spawning period of oysters, as well as of other Pelecypoda, depends upon climatic conditions. Thus the American oyster of Nova Scotia spawns only during the three or four warmest weeks of the year or not at all if the

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temperature of the water does not reach 20° C. (Nelson, '17), whereas in some parts of Chesapeake Bay the spawning of oysters was observed to begin at the end of May and continue until October (Loosanoff, '32). Orton ('20) points out that the breeding season of *O. edulis* of Norwegian waters continues for only a few weeks, while the oysters of the Gulf of Toranto breed from April to October. In other words, animals inhabiting cold waters have a breeding period of a shorter duration than individuals of the same species living in warmer seas.

The spawning reaction of *V. mercenaria* consists of the shedding of sperm or eggs into the surrounding water. The sexual products are first extruded into the suprabranchial chamber and then discharged through the excurrent siphon. During the spawning act in the cases observed the shells of both sexes remain wide and evenly open, indicating that the adductor muscles are not involved in the reaction. Consequently the reaction could not be recorded by a kymograph. In this respect the spawning reaction of clams appears to differ from that of female oysters because the reaction in the latter case is characterized by a series of rhythmical contractions of the adductor muscle which may be clearly recorded by means of a kymograph (Galtsoff, '32).

FIELD OBSERVATIONS

According to Belding ('12) the spawning temperature for *V. mercenaria* is 76–77° F. (24.4–25° C.). His conclusions are based upon the observations performed on animals kept under laboratory conditions. Spawning was recorded in five instances only. Belding found that in Massachusetts waters the spawning season of *V. mercenaria* extends from the middle of June to the middle of August. The writer's observations in Long Island Sound and its tributaries indicate that the spawning season of clams in those waters continues for a somewhat longer period than Belding gives for Massachusetts. As a rule, the clams of shallow water begin to breed considerably earlier than the animals living in the deeper parts of the Sound. For example, it was observed in 1934 and 1935 that the clams of Indian River began to discharge their spawn as early as the first week of June. Indian River, constituting one of the tributaries of Milford Harbor, is a shallow gulf, the bottom of which is almost exposed at low water stages. During the spring and summer the water there is always warmer than that of the adjoining harbor, and early in June temperatures as high as 27–28° C. have been recorded. Examination of clams collected in that locality in the middle of July showed that in many cases spawning had been completed. On the other hand, in Long Island Sound proper, the spawning generally begins very late in July and reaches its height during the latter part of August.

Figure 1 shows the bottom water temperature near Charles Island, Long Island Sound, from April, 1932, until December, 1935. These temperatures were recorded near and above the clam beds, the population of which was

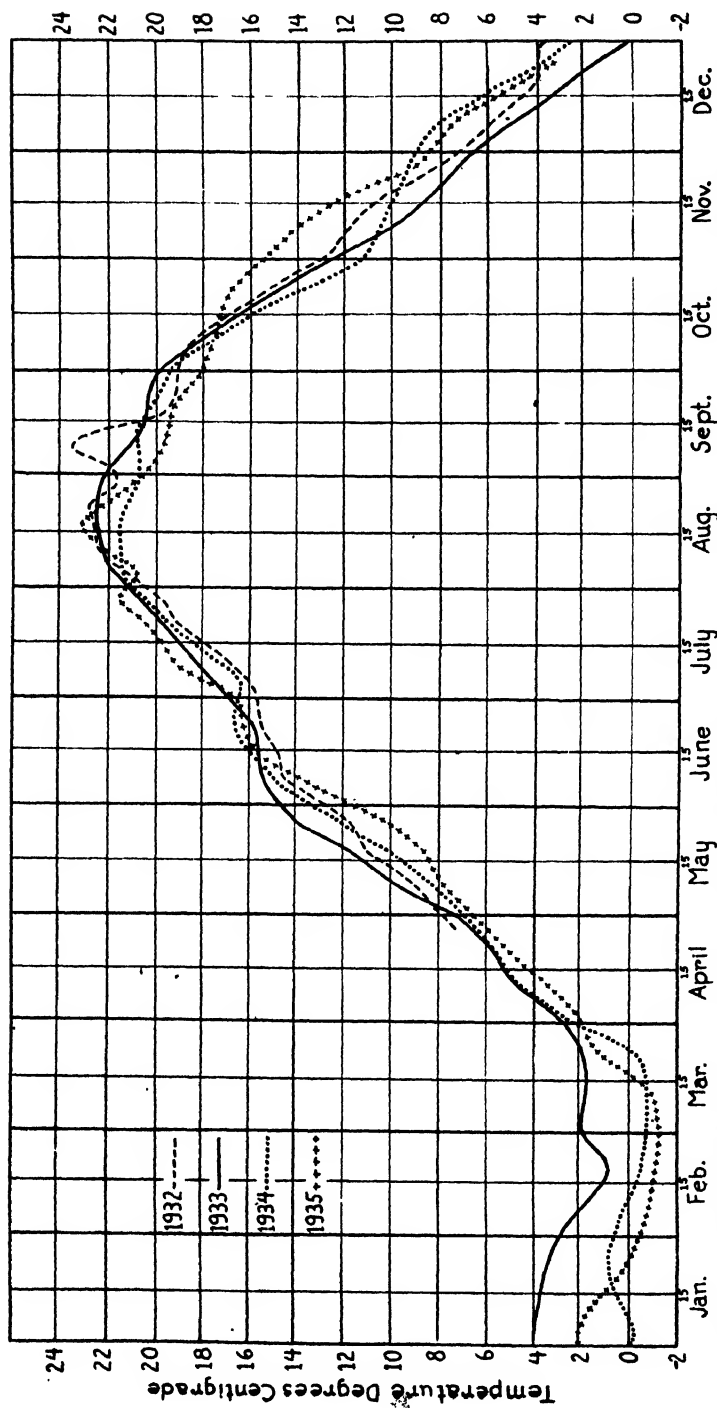


Fig. 1. - Bottom Water Temperature near Charles Island, Long Island Sound. April 1932 - December 1935.
FIG. 1 Bottom water temperature near Charles Island, Long Island Sound, April 1932-December 1935.

studied in regard to spawning activities. It may be seen from figure 1 that during the entire period of study the water temperature of that part of Long Island Sound never attained 25.0° C., which is considered by Belding ('12) as the minimum spawning temperature for *V. mercenaria*. The highest water temperature in Long Island Sound is usually reached in the middle of August, and begins to decline at the end of the same month. The height of the spawning activities of the clam population of our experimental bed always coincided with the highest temperature of the season. Three or four weeks later the majority of clams had completed spawning. In connection with the discussion of temperature inducing the spawning of clams on the experimental bed it should perhaps be indicated that the bed was located not far from the shore in a comparatively shallow place (8-12 feet of water at mean low water stage). Naturally, the temperature of the water above that bed was somewhat higher than that of the deeper portions of Long Island Sound. The writer, who had the opportunity to study the temperature changes of water in Long Island Sound for a number of years, has never observed a temperature higher than 23.5° C. at the depth of 25 feet or deeper. This fact was observed in connection with the studies of the biology of *O. virginica* which required the establishment of several experimental oyster beds located at different depths ranging from 8 to 45 feet. These beds were visited twice a week during spring and summer. The temperature of the water over the beds was measured by means of a deep-sea reversing thermometer, which was certified by the U. S. Bureau of Standards. In very few instances was a temperature of 23° C. observed in 25 feet of water or deeper and in no case was the temperature of 24.0° C. recorded. Nevertheless, the histological studies of clams collected from deep water early in September revealed that their sexual products had already been discharged. These facts lead to the conclusion that under natural conditions the spawning of *V. mercenaria* may take place at a temperature lower than 24° C.

Examination of gonads of animals collected in August from the natural beds showed that their spawning process is not a phenomenon of short duration. Histological studies revealed that different follicles of the gonad of the same animal contained sex cells in various quantities. Some follicles had already discharged their contents while others were still filled with mature eggs or spermatozoa. Apparently several days, or perhaps weeks, are required for an individual clam to complete its spawning. Furthermore, by examining a sample consisting of many animals collected at the same time and from the same place, it becomes evident that there is considerable difference in the spawning behavior of individual clams because some of the animals have their sex products completely discharged, while others still retain their spawn in various quantities. This indicates that the entire population of the same clam bed does not begin spawning at exactly the same time and that the spawning season of clams extends for a considerable period of time. Nelson ('28b), in his studies on *O. virginica*, arrived at virtually the same conclu-

sions. He observed the wide difference in the degree of maturity of oysters taken side by side from the same bed, and noticed that in New Jersey waters only a relatively small proportion of the oysters present take part in the first spawning of the season.

LABORATORY EXPERIMENTS

During the summers of 1933, 1934 and 1935, observations on the spawning of clams were carried on under laboratory conditions. On May 24, 1934, two out of four females spawned in an aquarium after being subjected to a temperature of 26.0° C. for two hours. The eggs discharged in the normal way were fertilized by the addition of a few drops of spermatozoa suspension, and began to develop. The temperature of the water over the bed which produced clams for this experiment was at that date 14.0° C., *i.e.*, 11.0° C. lower than the temperature which is considered critical for the initiation of spawning in *V. mercenaria*. May 24th was the earliest date at which the spawning of clams could be provoked by any means.

During June, July and especially in August, many animals were induced to spawn under laboratory conditions. The temperatures at which spawning took place varied from 23 to 30.2° C. There were two series of experiments devised to study the effect of temperature upon the spawning of clams. The usual method followed in the first series of experiments was to place the animal in a large vessel of sea water and proceed to warm the water at the rate of 1.0° C. every half hour until a temperature of 30.0° C. was reached. The initial temperature of the water at the beginning of the experiments was usually 22.0° C.

Individual clams showed great variability in their response to the increase in water temperature to and above the critical point. Few of the clams could be induced to spawn at the time of the experiment by raising the temperature of the water. On summarizing our observations it was found that only one animal in about every seven responded favorably and discharged spawn. Table I shows the number of animals used in the experiments and the temperatures at which some of them commenced spawning. The sex of all the animals used in this experiment was not determined. However, since among the adult clam population the sexes are represented in virtually equal numbers, it was assumed that among 379 clams used the sex ratio was approaching equality. It may be seen from table I that nearly all the animals that spawned at a temperature below 25.0° C. were males. The largest number of males spawned at 25–26° C. Females proved to be more resistant to the effect of high temperatures than males. Only 22 females were induced to spawn by the rise of temperature as compared with 32 males. At 24.0° C. only one female spawned and the greatest number of them spawned at 29.0° C. To avoid mutual stimulation during the experiments, each animal was kept in a separate vessel.

TABLE I. *Total number of adult clams exposed to temperatures ranging from 23.0 to 30.0° C., and number of clams of each sex commencing spawning at different temperatures*

Temp. ° C.	Number of clams used	Number of spawning animals		
		♂	♀	Total ♂ and ♀
	379			
23.0		2	0	2
24.0		2	1	3
25.0		6	2	8
26.0		6	4	10
27.0		5	3	8
28.0		5	3	8
29.0		3	6	9
30.0		3	3	6
Total	379	32	22	54

Another series of experiments was carried on in July and early August of 1934. In that series an attempt was made to establish the latent period of the spawning reaction induced by different temperatures. The temperature of the water in the vessel was brought to a desired point before the animal was placed in it. The temperature was then kept uniform until the end of the experiment. The experiment consisted of noting how soon the clams began to spawn after being placed in water of certain temperatures which ranged from 25.0° C. to 30.0° C. Ten clams were used in each experiment which lasted for four hours. At the end of that time all the animals which did not spawn were killed and their gonads examined to determine their sex and the state of development. Table II shows the results obtained from these experiments. It may be seen from the table that there is no significant correlation between the temperature and the number of animals spawned. It shows, however, three facts of importance: (1) Males are more easily provoked to spawn by high temperatures than females; (2) the average latent period of spawning reaction at temperatures 25–30° C. is shorter for males (46 min.) than for females (1 hr. 24 min.); and (3) at higher temperatures the latent period is generally, but not decidedly, of shorter duration than at low ones. Fortunately the sexes of the clams chosen for the experiment were represented in approximately equal numbers. Microscopical examination of the gonads of unspawned clams showed that all of them were apparently ripe. As compared with the first series of experiments, which consisted of inducing spawning by raising the temperature of the water 1.0° C. every half hour, the clams of the second series of experiments gave a larger percentage of spawners. In the first experiment only one out of every seven clams spawned, whereas in the second series every fifth individual responded. It is probable that the animals used in the two experiments were in various degrees of physiological maturity.

It is difficult to draw definite conclusions on the basis of the results obtained from the two series of experiments described above. There is no ex-

TABLE II. *Number and percentage of clams of opposite sexes spawned at different temperatures, and latent periods of the spawning reaction*

Number of clams used	Temp. ° C.	Spawned		Unspawned		Latent period
		♂	♀	♂	♀	
10	25.0	1	0	4	5	Male I 37 minutes
10	26.0	2	0	3	5	Male I 1 hour 30 min. Male II 45 minutes
10	27.0	2	1	2	5	Male I 1 hour 45 min. Male II 23 minutes Female I 2 hours 28 min.
10	28.0	1	1	4	4	Male I 30 minutes Female I 48 minutes
10	29.0	2	1	3	4	Male I 12 minutes Male II 55 minutes Female I 1 hour 16 min.
10	30.0	1	1	3	5	Male I 16 minutes Female I 1 hour 6 min.
Total		9	4	19	28	
Number of males used in experiment						28
Number of females used in experiment						32
% of males spawned						32
% of females spawned						12
Average latent period at temperatures 25-30° C.						Males 46 min.
Average latent period at temperatures 25-30° C.						Females 1 hour 24 min.

planation available as to why only a few clams spawned when subjected for hours to a temperature higher than the critical one. Histological examination of the gonads of some of the clams that refused to spawn indicated that they were ripe morphologically. Unfortunately, the important question of physiological ripeness could not be ascertained because in the case of *V. mercenaria* the usual methods of artificial fertilization always give negative results. Only those eggs that are discharged in the normal way can be fertilized by the addition of spermatozoa. Eggs obtained by cutting or rupturing gonads of the clam remain inactive. However, since many of the animals refusing to spawn were experimented with during July and August, that is during the normal spawning period of this species, it may be assumed that they were ripe morphologically and physiologically. Presumably in *V. mercenaria* some other factors in addition to temperature are necessary to provoke normal spawning. The behavior of the majority of unspawned clams was quite normal during the experiments and no difference could be observed in the general behavior of both groups of animals, *i.e.*, those that spawned during the experiment and those that refused to spawn. There appears to be no definite correlation between the rise in water temperature and the increase in the number of spawning clams (tables I and II). Significant facts revealed by these experiments are that in several cases the spawning of clams

of both sexes occurs below 25.0° C., which has been considered the critical temperature, and that males are more sensitive to a temperature stimulus than females.

A study carried on by Galtsoff ('26, '30, '32) on the physiology of the reproduction of oysters showed that mutual stimulation of the two sexes plays an important rôle in the spawning activities of those animals. In both sexes spawning could be provoked by the addition of a small amount of sexual products to the water. He often found that oysters which failed to respond to high temperatures readily responded to the addition of sperm or egg suspension. Experiments of a similar nature were performed on clams by the writer. Very few animals responded positively to stimulation by the genital products of the same or opposite sex. Again, males responded more often than females. The reaction of the animals spawned appeared to follow the all-or-none law, being independent of the concentration of the stimulant used. Spawning could never be induced by chemical stimulation at a temperature lower than 23.0° C. In this respect there is a difference between *V. mercenaria* and *O. virginica* or *O. gigas* because in two latter cases it was possible to induce males to spawn at a temperature of 12.0°–12.5° C., which is considerably lower than the usual spawning temperature for those animals (Galtsoff, '32, '33).

Due to the fact that in the majority of cases the spawning of stimulated clams occurred at a temperature of 24° C. or above, it was impossible to decide whether the reaction was provoked by the addition of genital products or by a rise in temperature. Furthermore, the average latent period of spawning reaction taking place after the addition of sperm or egg suspension was essentially the same as that observed in the experiments by which the spawning was induced by a rise in temperature. Very significant is the fact that only in a few clams could spawning be provoked by either a rise in water temperature, or by the addition of suspension of genital products, or by the combination of both methods.

The weak response of the clams to the addition of genital products is rather unusual as it is well known that in many Pelecypoda, when temperature alone is not sufficient to induce spawning, chemical stimulation by genital products of the opposite sex usually provoke the reaction. It seems, therefore, that the normal stimulus or rather stimuli which induce the act of spawning in *V. mercenaria* are still imperfectly known. Undoubtedly, both temperature and chemical stimulation are important in inducing the spawning reaction in *Venus* but their relative significance is not yet quite clear. More experimental work is necessary to clarify the nature of spawning reaction in clams. However, the case of *V. mercenaria* is not unique. Field ('22), studying *Mytilus edulis*, found that the rise in water temperature, addition of sexual products, transfer from water of high density to that of low density and back again, exposure to the air from one to three hours and then return to water, subjection to swift currents and then still water, gave no positive evidence of

influencing the act of spawning. All these methods were also tried on *V. mercenaria* but gave negative results. Thus, the nature of spawning stimuli of these two species remains unknown.

In connection with the spawning experiments, numerous attempts were made to fertilize the eggs obtained from female clams by artificial means. Regardless of the fact that the techniques employed were greatly varied, in not a single case were positive results obtained. To make certain that ripe eggs were used in the experiments on artificial fertilization, female clams were allowed to spawn normally for several minutes and then were taken from the water, quickly removed from the shells, and washed in sea water to remove all normally discharged eggs which could be found in the mantle cavity and gills. Immediately afterward portions of the ovaries were cut out and the ripe eggs squeezed into vessels of pure sea water. To the first batch of eggs thus obtained spermatozoa were added immediately. The second batch was washed in water several times before the addition of spermatozoa. The third batch was also washed three or four times and then divided into ten portions, to the first of which spermatozoa were added half an hour afterwards. To the next nine portions sperm was added at half hour intervals; thus, the last portion received sperm at the end of a 5 hour period. In all cases the results were negative. Microscopic examination revealed that while spermatozoa were actively swimming around or were attached to the egg membrane, the germinal vesicles of ova were intact. Not a single egg in the stage of formation of the first polar body or in later stages of fertilization could be observed. Apparently the inability of the germinal vesicle of the egg to break down outside of the ovary is responsible for the failure of artificial fertilization. Under normal conditions while the egg is still in the ovary the germinal vesicle breaks down and forms the spindle for the first polar body as is the case with a considerable number of other animals, both vertebrates and invertebrates. Undoubtedly, the contact of the clam egg with water does not provide a necessary stimulus for the dissolution of the germinal vesicle, the crucial step which renders the egg ready to be fertilized by the sperm.

SUMMARY

1. Studies of *V. mercenaria* of Long Island Sound indicate that under natural conditions the spawning of this species may take place at a temperature lower than 24.0° C.
2. Under laboratory conditions the spawning took place at temperatures ranging from 23.0 to 30.2° C. Nearly all the animals that spawned at a temperature below 25.0° C. were males. The largest number of males spawned at 25.0–26.0° C., and females at 29.0° C.
3. Males are more easily provoked to spawn by high temperatures than females. The average latent period of spawning reaction at temperatures 25.0–30.0° C. is shorter for males than for females. At higher temperatures

the latent period is generally, but not decidedly, of shorter duration than at low ones.

4. Spawning could never be induced by chemical stimulation or by any other methods at a temperature lower than 23.0° C.

5. Only in a few cases could spawning be provoked by either a rise in water temperature, or by addition of suspension of genital products or by the combination of both methods. The nature of spawning stimuli of this species remains doubtful.

6. Numerous attempts to fertilize the eggs obtained from females by artificial means always gave negative results.

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PLANT SUCCESSION ON SOLONETZ SOILS IN WESTERN NORTH DAKOTA

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INTRODUCTION

A prominent feature of western North Dakota landscape is the pitted nature of the surface in many areas (fig. 1). These areas are called various names, such as "scabby spots," "slick spots," "burnouts," and in accordance with recent soil science "solodized solonetz complexes." In the aggregate they occur on thousands of acres. Scientific planning for the use of such land is dependent in large measure upon data regarding their origin, fate, and relationship to the natural vegetation. The pits are a few inches to about a foot deep, irregular in outline, and vary in area from a few square feet to a hundred or more. They may be bare or covered with a thin stand of weeds, low shrubs, or grasses, and are surrounded by denser stands of grassland, composed chiefly of grama grass. The cycle of plant destruction and plant succession occurring in these scabby areas is dependent upon the initial edaphic causes which are operating. In a recent paper Kellogg ('34) explained a theory which describes the chemical processes that may be the chief initial causes. This explanation and the characteristics of the various stages in the development of the soil are summarized in the following paragraph.

According to Kellogg the upper layers of the *normal* soil in western North Dakota are characterized by crumb to prismatic structure, and are friable without difficulty. The base exchange is largely saturated with divalent cations, colloids are flocculated, reaction is about neutral, and calcification is the dominant process. An excessive concentration of soluble salts, caused usually by capillary rise from the water table, leads to the development of *solonchalk* (saline soil), which is usually characterized by the replacement of some divalent cations by monovalent, especially sodium. The colloids remain flocculent, the reaction is not highly alkaline, and the surface may become white and puffy; *salinization* is the dominant process. Improved drainage of the solonchalk which contains sodium salts brings about the development of the *solonetz* (alkali soil) through the removal of the excess soluble salts. The relatively large amount of exchangeable sodium saturates the

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base-exchange colloids which become deflocculated. As a result the structure becomes hard and prismatic and the soil has a highly alkaline reaction due to hydrolysis of the sodium-saturated colloids. *Solonization* is the dominant process. The downward movement of the dispersed colloids and the reduction in the exchange capacity (*solodization*), resulting in an A_2 horizon that is light colored, platy in structure, and light in texture, characterizes the final stage or *soloth*. The B_2 horizon remains dark, hard, and columnar, but as the process of solodization continues the columnar structure may break down and both horizons may become somewhat acid. The light, loose A_2 horizon may wash or blow away, exposing the hard B_2 horizon on the surface of the pit. The removal of the mobile colloids and the reactions of plants, which now invade, lead to reconstruction of the soil and calcification becomes increasingly important.



FIG. 1. View of a solodized solonetz complex in the valley of the Heart River about one mile north of South Heart, North Dakota. All stages in succession from bare areas to nearly climax occur in the gently sloping foreground.

REVEGETATION OF THE BARE PITS

It appears that grama grass, *Bouteloua gracilis*, is usually able to persist as the major dominant during the course of soil development from the normal, or near-normal soil, through the solonchalk and solonetz stages to the soloth stage. This is illustrated at the left end of the trench in figure 2. Associated with grama grass are *Plantago purshii*, *Plantago elongata*, *Carex stenophylla*, *Agropyron smithii*, *Salsola pestifer*, *Lepidium apetalum*, *Chenopodium leptophyllum*, *Atriplex argentea*, *Poa buckleyana*, *Festuca octoflora*, *Malvastrum coccineum*, *Artemisia frigida*, and *Stipa comata*. The number of weedy species in this list is indicative of disturbance or variation in the normal relation-

ships of vegetation and soil. If the concentration of salts during the solonchalk stage becomes too great *Agropyron smithii*, *Distichlis stricta*, or *Puccinellia nuttalliana* may replace grama grass as the dominant.

This vegetation is destroyed during the erosion of the A_2 horizon of the solonch stage (fig. 2). Frequently a portion of the hard B_2 horizon also erodes before the invading vegetation becomes dense enough to hold the soil. The erosion is marked by a pronounced step, which varies in height from a few inches to over a foot. The most common species, usually occurring consider-



FIG. 2. At left end of trench is shown a typical solonch stage (light-colored, loose A_2 horizon; dark-colored hard B_2 horizon) with vegetation cover dominated by *Bouteloua gracilis*. Bare area, caused by erosion of A_2 horizon and destruction of vegetation above the step, is being invaded by a few forbs and shrubs; followed at right by first grass stage (*Agropyron-Puccinellia-Poa*), and at right end of trench by buffalo grass sod, the second grass stage. About 15 miles south of Belfield, North Dakota.

ably scattered on the steps, are such weedy plants as *Salsola pestifer*, *Polygonum aviculare*, *Lappula occidentalis*, *Atriplex nuttallii*, and *Chenopodium leptophyllum*. In clay soil near Rhame *Artemisia tridentata* appeared to be confined in its distribution chiefly to the steps or close to them.

The surface layer of the bare area varies from easily-friable crumb (fig. 2) to compact clay which cracks into irregularly polygonal blocks upon drying (fig. 3). Below the crumb-like mulch, if it is present, are horizons, usually of clay, showing more or less prismatic structure, and varying in friability. Mild effervescence, indicating the presence of carbonates, begins at a depth of

3 to 4 inches and becomes more pronounced with depth. The colloid content and water-holding capacity of the soil are high, pH about 8.0, and sodium content low to medium. Water penetration is slow and shallow. Because of these characteristics invasion and aggregation by plants are difficult and slow, and erosion continues.

The kinds of species invading these bare areas vary, depending upon such factors as soil structure, amount of sodium in the soil, drainage conditions, kind of parent plants near enough to supply the disseminules, and moisture and temperature conditions prevailing during germination and growth of seedling invaders. The most common invaders are *Polygonum erectum* L., *Lepidium densiflorum* Schrad., *Atriplex nuttallii* S. Wats., *Atriplex argentea* Nutt., *Plantago elongata* Pursh, *Opuntia fragilis* (Nutt.) Haw., *Iva axillaris* Pursh, *Salicornia herbacea* L., *Distichlis stricta* (Torr.) Rydb., *Gutierrezia sarothrae* (Pursh) Britton and Rusby, *Grindelia squarrosa* (Pursh) Dunal., *Suaeda depressa* (Pursh) S. Wats., *Salsola pestifer* A. Nels., *Agropyron smithii* Rydb., and *Eriogonum multiceps* Nees.

The roots of these plants are mostly in the surface foot and the working depth is at about 10 inches. Reactions of the roots increase the porosity and flocculation of the soil, add to the organic matter, and in other ways tend to improve the structure and other soil conditions.

First grass stage

The soil in this stage is similar to that in the preceding. The surface inch or so often has a platy structure and clay texture. It is brittle, filled with fine pores, and crumbles readily to dust. Below this the clay forms irregular and poorly defined prisms which break up into fairly hard angular fragments one-fourth inch or smaller in diameter. Small pores extend 2 to 4 inches into the soil and vertical cracks are found to a depth of 2 feet or more. The working depth of the roots usually extends to 18 to 24 inches. The surface soil contains a trifle less sodium, and the pH is slightly less than in the soil of the first stage. Effervescence, somewhat stronger than in the horizons of the bare area, begins mildly at a depth of 2 to 4 inches and becomes strong below a depth varying from 8 to 20 inches. The colloid content (42 to 68%) is slightly lower than in the bare areas, loss on ignition (5.1 to 8.0%) slightly higher, the reaction about the same (pH 7.7 to 8.1), carbonates about the same (6.5% near the surface to 14.5% below 20 inches), and the sodium content very low to low.

This soil affords only slightly better growing conditions than in the bare area. The increased number and greater penetration of roots of grasses, however, hasten the rate of soil reconstruction. The soil is less subject to wind and water erosion. Compared to the bare areas penetration of water received from rainfall and melting snow is probably increased; and the death and decay of numerous small roots each year improves chemical and physical conditions in the surface foot particularly.

Perennial grasses whose leaves extend to heights of 8 to 12 inches characterize this stage. The most important of these are *Agropyron molle* (Scribn. and Smith) Rydb., *Puccinellia nuttalliana* (Schultes) Hitchc., *Agropyron albicans* Scribn. and Smith, *Agropyron smithii*, *Schedonnardus paniculatus* (Nutt.) Trelease, and *Distichlis stricta*. Common forbs are *Astragalus*

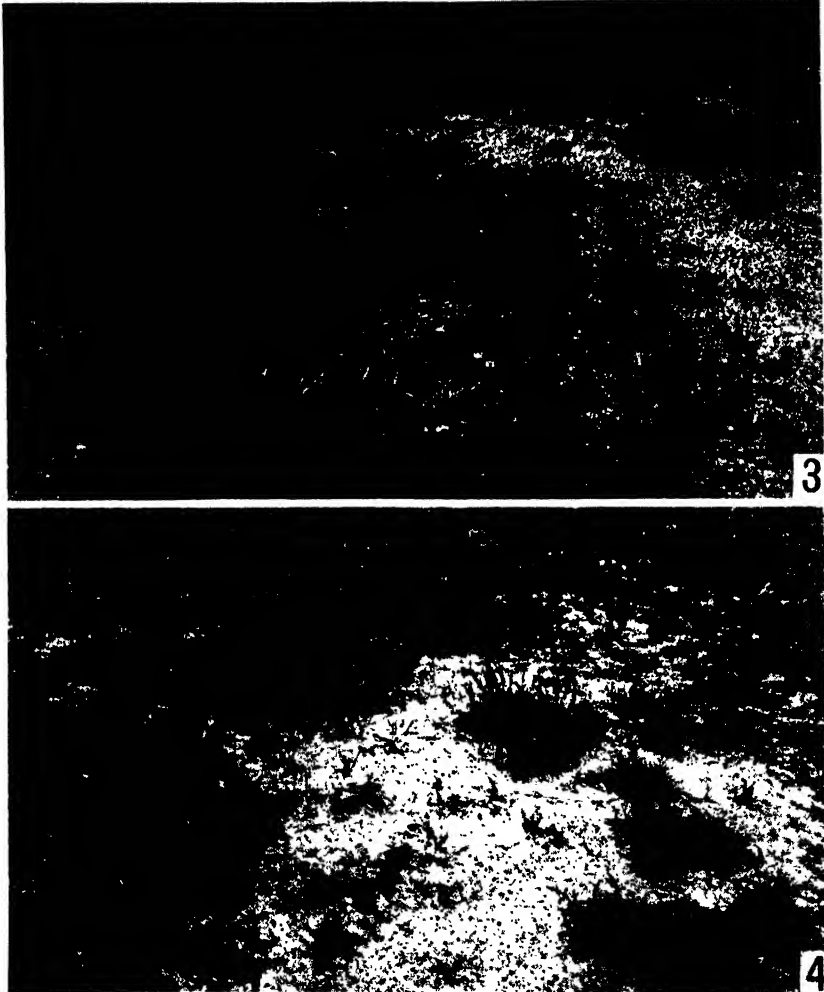


FIG. 3. First grass stage (chiefly *Agropyron molle* and *Puccinellia nuttalliana*) on hard clay of B₂ horizon of soloth near Rhame, North Dakota.

FIG. 4. Bare areas being invaded by *Distichlis*, *Salsola*, *Gutierrezia*, *Atriplex nuttallii*, and *Artemisia tridentata*; followed by *Agropyron molle* and *A. albicans*. Behind this is the buffalo grass stage and, in extreme upper left corner, grama grass above the step. *Opuntia polyacantha* in first grass stage in left foreground near Rhame, North Dakota.

goniatus Nutt., *Artemisia frigida* Willd., *Aster multiflorus* Ait., *Polygonum erectum*, and other species remaining from the mixed forb and low shrub stage.

Second grass stage

The surface, one-half to one-inch layer in this stage, is clay in texture and is darker colored than in the preceding stage. The small crumb structure is rather easily friable to powder. Below this, to a depth of 5 to 8 inches the dark brown clay shows poorly defined prismatic structure. It digs out into irregular fragments up to about one-half inch across which are friable with some difficulty. Below this are lighter colored layers of clay, more or less mottled with white. The clay breaks into irregular, angular pieces which are friable with difficulty. Parent material occurs at a depth varying from 26 to 32 inches. Effervescence begins moderately at 4 to 5 inches and becomes strong at 8 to 10 inches. Roots are abundant from the surface inch to the working depth at 25 to 30 inches. Colloidal content and pH are slightly lower in this stage than in the first grass stage. The sodium content has become greatly reduced, varying from zero to very low in the upper 20 inches of soil. The calcium content is slightly higher than in the preceding stage while losses on ignition and carbonate contents are similar.

The dominant in this zone is buffalo grass, *Buchloc dactyloides* (Nutt.) Engelm., which usually forms a fairly dense mat. Other grasses occurring here, but of minor importance, are *Poa buckleyana*, *Agropyron smithii*, *Bouteloua gracilis* (H. B. K.) Lag., *Koeleria cristata* (L.) Pers., and the sedge *Carex stenophylla* Wahl. Common forbs are *Plantago purshii* R. and S., *Lepidium densiflorum*, *Psoralea argophylla* Pursh, *Chenopodium leptophyllum* Nutt., *Aster multiflorus*, *Linum rigidum* Pursh, *Hedeoma hispida* Pursh, and *Oxytropis lambertii* Pursh.

Climax stage

The decrease in the sodium content of the soil, the increase in calcium, and the numerous reactions caused by the abundance of grass roots result in a normal soil unless salinization begins again before reconstruction is complete. As long as topography, parent material, and other factors favor the continuation of the processes which produce the scabby spots it is unlikely that the climax will be attained. Salinization, solonization, and solodization, followed by erosion, may begin again in the first or second grass stage. Once a scabby area begins to develop it appears that it will be subjected for a long period of time to these soil processes and incomplete seres. There will be a continuous repetition of the cycle of salinization, solonization, solodization, erosion, invasion, aggregation, reaction, succession, and partial reconstruction of the soil. In time, however, the climax may be reached and a normal soil developed.

The normal soil (Kellogg, Hanson and Whitman) is dark brown to depths of 4 to 7 inches (A horizon). This portion has a coarse, easily friable crumb

structure. Below this, and extending to depths of 20 to 24 inches the soil is lighter in color. The structure is more or less prismatic, falling into pieces that are easily friable in the upper portion but somewhat less friable in the lower portion. The horizon below this is more compact, less friable, and lighter in color. The roots are numerous to depths of 2 to 2.5 feet; the working depth occurs at depths of 2.5 to 3 feet. The soil colloids are low to moderate, ranging usually from 12 to 30 per cent. The dark soil extends to depths of 17 to 33 inches, loss on ignition is low, reaction is slightly acid (pH 5.8 to 6.7) to depths varying from 6 to 38 inches, carbonates (2-15%), and total soluble salts (281 to 680 p.p.m.) are low, effervescence begins at 13 to 60 inches, calcium content is medium to high, and sodium is lacking.

The dominants are *Bouteloua gracilis*, *Stipa comata* Trin. and Rupr., *Carex filifolia* Nutt., *Carex stenophylla*, and *Agropyron smithii*. Other common species are *Malvastrum coccineum* Nutt., *Carex pennsylvanica* Lam., *Chenopodium leptophyllum*, *Lygodesmia juncea* (Pursh) D. Don., *Plantago purshii*, *Lepidium densiflorum*, *Hedcoma hispida* Pursh, *Artemisia gnaphalodes* Nutt., *Artemisia frigida*, *Echinacea angustifolia* DC., *Psoralea argophylla*, *Gaura coccinea* Nutt., and *Allium reticulatum* Don.

SUMMARY

Plant succession on bare areas resulting, according to the theory described by Kellogg, from salinization, solonization, and solodization on solonetz complexes in western North Dakota is described.

The invaders on these bare areas are weedy forbs and low shrubs.

The second stage in succession is characterized by grasses as *Agropyron*, *Puccinellia*, and *Poa buckleyana*.

The third stage is dominated by *Buchloe dactyloides*, which is followed by the climax in which *Bouteloua gracilis*, *Stipa comata*, *Koeleria cristata*, *Agropyron smithii*, and *Carex* spp. are the chief dominants.

The course of succession toward the climax may cease at any stage due to the reoccurrence of salinization. All parts of an active solonetz area show continuous repetitions of the cycle of salinization, solonization, solodization, erosion, invasion, aggregation, reaction, succession, and partial reconstruction of the soil.

During the course of plant succession from the bare area on the exposed B₂ horizon of the soloth toward the climax vegetation on normal soil the colloids change from the dispersed condition to flocculated, and the hard, columnar horizon becomes more or less prismatic and readily friable.

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ATTACHMENT OF THE LARVAE OF *OSTREA GIGAS*, THE JAPANESE OYSTER, TO PLANE SURFACES

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A variety of environmental factors may influence the survival of the oyster during the critical period when the free-swimming larvae become attached to fixed objects and metamorphose into the adult form. Recent investigations by Hopkins ('35) have shown that the angle of the surface to which the larvae attach has an important relationship to the intensity of setting of the larvae of *Ostrea lurida*.

Observations of the setting of the Japanese common oyster, *Ostrea gigas*, transplanted to Puget Sound, showed that a large majority of the young oysters were attached to the under surfaces of shells on the oyster beds. It was thought that a reaction of the larvae similar to that of *O. lurida* might explain this. The present experiments were, therefore, undertaken to ascertain the effect, if any, of the angle of surface on the setting of *O. gigas*.

MATERIAL AND METHODS

The Japanese common oyster has been introduced into numerous bays on the Pacific coast of the United States. In a few of these localities, the species has become acclimatized and reproduces readily. The present experiments were carried out in Quilcene Bay in Puget Sound, since, in this locality, the water is very clear and free from silt, reducing the interfering factor of differential silting of different surfaces to a minimum.

Plates of clear window glass, as used by Hopkins ('35), were employed. The 8 by 10 inch plates were held in frames of $\frac{1}{2}$ inch mesh galvanized hardware cloth. The frames could be wired together so as to hold the plates at any desired angle on the oyster beds.

Concrete-coated cardboard spat collectors were also utilized. These collectors consist of cardboard egg-crate fillers which are dipped in a mixture of cement and sand and allowed to cure for several days before being placed in the water. The collectors were suspended from a float which did not go dry at any time. They were suspended eight to fifteen inches below the surface of the water in such a manner that part of the surfaces were horizontal and the rest were vertical.

ATTACHMENT TO GLASS PLATES

In order to determine the relative intensity of setting on plane surfaces held at different angles, all surfaces being equally clean, one hundred and fifty

glass plates were placed on the oyster grounds. They were placed on the beds near mean low water level in a locality where the tidal current was unobstructed. Thirty plates were set in each of three positions: horizontal, at 45 degrees to the horizontal, and vertical. Fifteen plates of each of the latter two groups were placed parallel to the direction of the tidal current, while the remaining fifteen were placed transverse to the current's direction. The entire group of plates were placed close together in a small area to insure comparable results. The plates were left on the oyster beds for five days, then removed and the attached oyster larvae were counted under a binocular microscope. During the time when the plates were in the water, very little silt accumulated on any of the surfaces. Differences caused by differential silting of various surfaces were, therefore, negligible or absent.

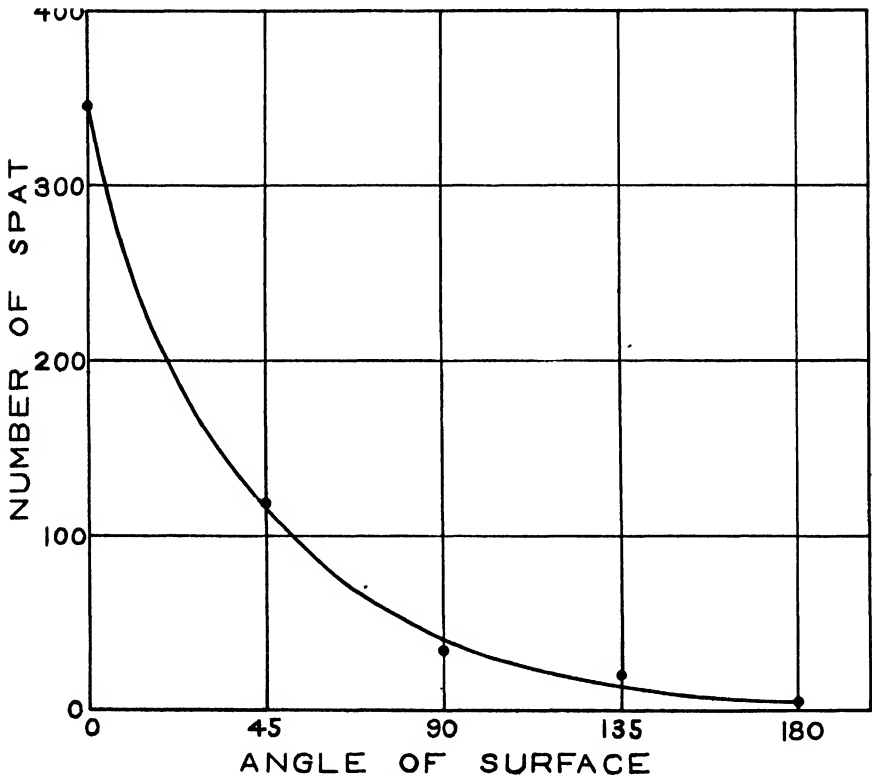


FIG. 1. Number of spat attaching on plane glass surfaces (2400 sq. in.) held at different angles.

The numbers of larvae attaching on the different surfaces are given in table I. In this table, and in figure 1, the under horizontal surface is designated 0°, the upper horizontal 180°. The lower and upper surfaces of the diagonal

TABLE I. *Number of spat attaching to plane glass surfaces held at different angles*

Angle of surface	Area sq. inches	No. spat	Av. spat per 2400 sq. in.
0°	2400	346	346
45° ¹	1200	75	119
45° ²	1200	44	
90° ¹	2400	39	35
90° ²	2400	31	
135° ¹	1200	12	
135° ²	1200	9	21
180°	2400	6	6

¹ Parallel to direction of current.² Transverse to direction of current.

plates are considered as 45° and 135°, respectively. Both surfaces of the vertical plates are considered as 90°.

An examination of table I shows that definitely more spat were found on the surfaces parallel to the current than on the transverse surfaces. This is, undoubtedly, as concluded by Hopkins ('35) for *O. lurida*, ascribable to the larger amount of larvae-bearing water passing over the surfaces parallel to the current.

In figure 1, the numbers of spat attached per unit area are plotted as a function of the angle of the surface. A definite relationship is at once apparent, the points falling very nearly on a hyperbolic curve. Thus, there is a functional relationship between the intensity of setting and the angle of the surface to which the larvae attach. The set is greatest on the 0° surface, and decreases as the angle of surface approaches 180°, at which angle the frequency of attachment reaches a minimum. The number of spat is taken as the average of the surfaces transverse and parallel to the current. If table I is consulted, however, it will be seen that if the counts on the parallel surfaces alone were used, the general shape of the curve would not be appreciably altered.

SETTING ON SPAT COLLECTORS

Counts were made on concrete-coated cardboard spat collectors which had been suspended in the water, for one month, from a float in such a manner that part of the surfaces were horizontal and the rest were vertical. The collectors, after being dried, were cut apart and the number of spat on each piece counted and tabulated according to the angle of the surface to which they were attached.

The counts on spat collectors are given in table II, together with the areas covered. On the under horizontal surfaces, about three times as many spat were found as on the vertical surfaces, and about five times as many as on the upper horizontal surfaces. This is in agreement with the results of the experiments with the glass plates. On the glass plates, however, about ten times as many spat were found on the under horizontal as on the vertical sur-

TABLE II. *Number of spat attached to concrete-coated cardboard spat collectors left in water one month*

Surface	No. spat	Area in sq. in.	Spat per 100 sq. in.
Lower horizontal	2610	826	316
Vertical	2114	1820	116
Upper horizontal	548	826	66

faces, and about fifty times as many as on the upper horizontal surfaces. Since the collectors were in the water for a long period, this increased proportion of spat found on the upper and vertical surfaces of the collectors might be due to greater silting of the upper surfaces, or to a differential mortality rate of the spat on the different surfaces. The difference, however, is probably to be attributed to the irregularity of the concrete surfaces. The grains of sand in the concrete are much larger than the oyster larvae. The rough surfaces of the collectors, therefore, prevent any surface from being either totally vertical or horizontal. The glass plates, left in the water for a short time only, are alone an adequate means of testing the exact effect of the angle of a plane surface on the frequency of attachment.

DISCUSSION

The present experiments demonstrate that there is a functional relationship between the frequency of attachment of the larvae of *Ostrea gigas* and the angle of the surface to which larvae attach. The frequency of attachment is least on the upper surfaces and becomes increasingly greater as the angle of surface approaches 0°, or the under horizontal. On glass plates held at known angles, the under horizontal surfaces caught nearly ten times as many spat as the vertical surfaces and over fifty times as many as the upper horizontal.

This relationship between intensity of setting and angle of surface is essentially the same as that previously found by Hopkins ('35) for *Ostrea lurida*. There is, however, considerable difference in the behavior of the two species. Hopkins wrote (p. 85), "On plane glass about 100 times as many spat were caught on the under horizontal as on vertical surfaces, while almost none were attached to upper horizontal surfaces." In the present experiments only ten times as many spat set on the under horizontal as on the vertical surfaces, while appreciable numbers were also found on the 135° and 180° surfaces. There seems, therefore, to be a specific difference in the behavior of the two species in the respect that the set of *O. gigas* on the upper and vertical surfaces is proportionately greater than that of *O. lurida*.

This setting behavior of oyster larvae might be ascribed to either a negative geotropism or to the purely mechanical factor of the swimming position of the larvae, where the foot and velum are uppermost, and would, therefore,

most often, fortuitously, come in contact with the under surfaces. Hopkins ('35) suggested that the latter is the proper explanation. The difference observed in the behavior of *O. gigas* and *O. lurida* might not, however, be entirely explained on this basis. The negative geotropism of both *O. lurida* and *O. gigas* is well known (Amemiya, '28; Hori, '33). Amemiya, working with cultures of *O. gigas* larvae, found that the swimming larvae have a strong tendency to swim upward to the surface of the water, often forming dense clusters there. He was unable to correlate this behavior with any external cause, such as light intensity or oxygen content of the water, and concluded that the behavior is due to an "instinctive habit of the larvae." Such a tropism might be sufficient to explain the setting behavior described.

SUMMARY

Experiments with glass plates and concrete-coated cardboard spat collectors demonstrated that the majority of the larvae of *Ostrea gigas* attach to the under surfaces. On glass plates, ten times as many spat attached on the under horizontal as on vertical surfaces, and fifty times as many as on upper horizontal surfaces.

A functional relationship exists between the angle of surface and frequency of attachment of the spat, the points falling on a hyperbolic curve.

This setting behavior might be attributed to the upward position of the foot of the swimming larvae. It is, also, quite possibly due to negative geotropism of the larvae.

The setting behavior of *Ostrea gigas*, in regard to intensity of setting as related to angle of surface, is similar to that of *Ostrea lurida*, previously studied, but presents specifically different characteristics.

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PROBLEMS OF MEASURING FORAGE UTILIZATION ON WESTERN RANGES ¹

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In order to maintain range forage production at its highest level, and restore depleted ranges, the better forage plants must be used properly. But what is proper use? For the practical range administrator the answer requires a knowledge of the resistance to grazing of several hundred important species which furnish the bulk of the feed and afford most satisfactory watershed protection. However, in a land that requires from 20 to 100 or more acres to support a cow yearlong, the area that can be inspected with necessary frequency by one stockman or forest ranger is so small a proportion of the whole that the actual degree of utilization each season or year is necessarily very difficult to determine. In fact, except on very small study plots or pastures, degree of utilization is commonly based almost entirely on judgment acquired from experience. But when continued productivity or gradual death of a good forage grass may depend upon a difference in foliage removal of as little as 10 per cent, a more accurate measurement of utilization is necessary. That is why the Forest Service, through its Division of Range Research and six western forest and range experiment stations, is initiating a special project to formulate sound utilization standards and simple practical methods of measuring degree of forage utilization.

An infinite number of questions must be answered in the setting up of utilization standards for any particular range unit. For example, what are the species that do or should furnish most of the forage at different seasons of the year? What are their life histories, and how do the different classes of livestock relish them? What is the natural plant succession, how is it affected by varying degrees of grazing, and what stage can or should be maintained under grazing use? Even when proper utilization has been determined for a species or type under one set of conditions, what adjustments are necessary when the type is depleted severely, and what precautions are necessary for extreme drought or where special land services such as watershed protection, timber production or wildlife are important or dominant? What are the absolute or relative nutritive values or poisonous properties involved?

These problems are especially difficult as a result of the wide variety of the range resource, both as to composition, form, habitat, and in production

¹ Paper read at the Atlantic City Meeting of the Ecological Society of America, December, 1936.

one year with another. Range plants include representatives of every phylum and nearly every life form. Furthermore, the variety of animals feeding on this vegetation is no less striking. For example, on the National Forests the domestic animals permitted to graze include not only cattle, horses, sheep and goats, but also some hogs and even a few herds of turkeys. And these are in addition to all the big game and other wildlife, including rodents and insects, that live on the range.

Through the past 30 years the Forest Service has accumulated a mass of information relating to range management, most of which bears either directly or indirectly on forage utilization. At one time or another, nearly every ranger district in the West has had measurements of some kind: quadrats, enclosures, phenological observations, grazing capacity tests, actual stocking records, range surveys and inspections, or other information relating to range management. Also, experiments under the Division of Range Research extending as far back as 1912 at the Great Basin Station in central Utah, and since 1915 at the Jornada and Santa Rita Experimental Ranges in the Southwest, have brought out important results. The Forest Service Range Research organization is giving increasing emphasis to finding answers to the questions of actually measuring utilization and determining resistance to grazing, applicable not only to the 88 million acres of National Forest ranges, but to all the major range types in the West.

The immediate work in this utilization study is to evaluate all of the pertinent data available, both in the research and administrative offices of the Forest Service, and in other federal and state and private agencies. Even though the analysis of existing information yields helpful results of immediate use to the practical range administrator, a long-time program of fundamental research in range plant ecology, physiology and economics, as well as animal husbandry, is necessary to furnish final solutions to many of the more complicated problems. The Forest Service already has some 15 branch stations, about evenly divided inside and outside the National Forests, where range research is now under way, representing all of the broad vegetative types on the western range. Further studies to get at the utilization problem more specifically are already being initiated at several of these work centers. A typical set-up is the Desert Experimental Range, a branch of the Intermountain Forest and Range Experiment Station, in western Utah. On this 55,000 acre tract several possible ways of measuring utilization are under investigation, including clipping studies, grazing capacity and forage preference studies, studies of the effects of climate, soils, etc., and forage removal and its effect on plant nutrition and maintenance. At several work centers, these studies are in cooperation with state experiment stations or other public or private agencies.

One of the difficulties in developing satisfactory utilization standards is illustrated by figure 1, which shows the wide variation in forage year by year

as a result of climate on a mountain range in central Utah (Campbell, '35). At the same time, the figure shows one possible way of expressing proper utilization in terms of forage production, which can be converted into grazing capacity. The upper line shows average forage production, but there were six of the eleven years below the average, and three of these were a third or more below. Stocking the range on the basis of average production or above, as is often done, means short feed in about half of the years, unless the shortage is made up with costly supplemental feeding. Wise range management, therefore, indicates stocking at a point somewhat less than average. In this case, as shown by the heavy lower line, conservative stocking appears to be about 20 per cent below the average forage production, to permit the same

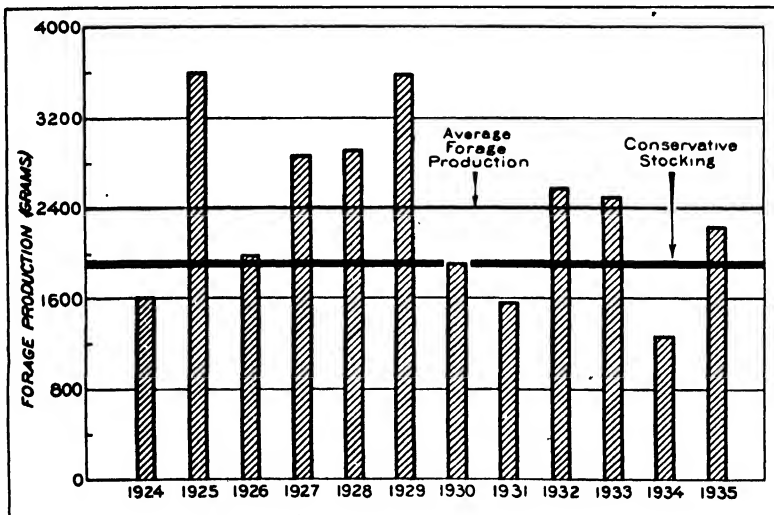


FIG. 1. Fluctuation in production of mixed perennial grasses on a square-rod plot in central Utah. Conservative stocking of the range must be based on proper utilization of the forage plants and be sufficiently below average production to furnish adequate feed in all but the lowest years.

number of livestock to obtain feed on the range in all but the most severe drought years without injury to the range or excessive costs to the producer.

An example of another type of tentative utilization standard will illustrate more specifically the kind of information needed. At the Jornada Experimental Range in southern New Mexico, clipping studies of black grama, *Bouteloua eriopoda*, have shown that under conditions found there the species will not withstand annual removal of the stems and leaves to a height of two inches. Other studies of grazing capacity and natural revegetation indicate that proper utilization of black grama should leave a stubble of approximately two inches plus about 15 to 20 per cent of the vertical stems and all the hori-

zontal stolons (fig. 2), since the principal means of starting new plants is through vegetative reproduction. On more compact soils, or under higher rainfall (as on the Santa Rita Range in Arizona), the plants appear to withstand a closer degree of utilization. On steep slopes or looser soils, a lesser degree of utilization might be necessary to minimize erosion. Of course there are severe drought years when large numbers of plants die, even if protected from grazing (Nelson, '34), and it would be best for the plants if no grazing of the short growth were allowed, but such ideal management is not often possible in actual field practice. However, the formulation of similar utiliza-



FIG. 2. Diagrammatic representation of a black grama tuft before and after being properly grazed. Note provision for vegetative reproduction.

tion standards for many more additional key species on western ranges is necessary to bring about their proper use, restoration, and maintenance. This information must be determined not only by broad types, but also by regions because the same plant may be relished in one type and not in another. For example *estafiata*, *Artemisia frigida*, is good spring sheep feed in northern New Mexico, but is eaten only very sparingly and is considered an indicator of overgrazing in the northern great plains.

Just how such standards can be most simply expressed, and methods of actually measuring utilization (instead of guessing) in terms of such standards so that the practical administrator can use the results obtained—this is

a distinct phase of the problem and must be worked out as research arrives at definite fundamental conclusions. The important point is that range forage utilization must be measured more accurately, and proper utilization must provide for maintenance of all the services of the land, not only forage for domestic livestock and wildlife, but also watershed protection and timber reproduction.

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REVIEWS

THE FACTOR OF MOUNTAINS¹

"Mountain Geography, a Critique and Field Study" is an advanced functional study of the interrelations of mountains on the one hand, certain climates, plants, domestic animals, and men on the other hand. It is not ecological but geographic. "We are not here concerned," says Professor Peattie, "to present a complete discussion of climatology" (or plant and animal ecology. E. F. H.). "Only those aspects which are of human importance are discussed, and the treatment is thus truly geographic." The book is treated here from the view-point of the nearest branch, human ecology. This, we consider, differs from functional geography only in that its creators aspire to make it as wide in scope and intense in synthesis as plant and animal ecology.

The opening chapters deal with mountain temperatures; humidity and precipitation; winds, clouds, and sun respectively. They give, in an incisive, compact form, the principles and formulæ for the understanding of these factors as they occur in conjunction with the various shapes, masses, elevations, compositions, etc., of mountains. Thus far this study coincided completely with the needs of the whole science of ecology. The fact that the book is based to the extent of about 75 per cent on the abundant studies of the Alps and Pyrennees, only 25 per cent on the relatively meager studies of other mountains has but small effect on the general applicability of the study of inorganic factors except in regard to volcanoes, whose study is not included in this work.

In the next two chapters the complex influences on vegetation of wind, shade, altitude, slope, etc., are portrayed in such a functional, quantitative and qualitative manner as to reduce the concept of vegetation zones to the status of a working hypothesis rather than, in general, a statement of existing fact. Principles according to which hypothetical vegetation zones are abandoned or maintained by mountain plants seem clearly stated and generally applicable. However, the treatment of the *specific* ways in which plants do so is not significant except for the few plants which affect Western men. All study of domestic animals is omitted in spite of their importance to many mountaineers in all continents. This and many other omissions symptomize the vastness of the subject, not the value of the book except in regard to its somewhat ambiguous title.

¹ Peattie, Roderick. 1936. Mountain Geography, A Critique and Field Study. 257 pp., 65 figures. Harvard University Press, Cambridge, Massachusetts. \$4.00.

The last five chapters of Professor Peattie's work have the provinciality and interrupted functionalism of a pioneer study. Its generalizations are not based upon sufficient, widely spaced samples to bear out the universality often imputed to them. The study of density and distribution of Alpine peoples, for instance, does not hold very well for New Guinea; the study of seasonal migrations in the Alps does not hold good for the Balkan Mountains, and so on. The synthetic effort in this part of the book is inadequate for the achievement of complete functionalism. For instance, the essentially low living standard, the tremendous effort, the great vitalizing qualities, and the mental pathology of rural mountain life are all stated, but are nowhere correlated. However, the synthesizing qualities of regional studies are cleverly utilized, correlating and evaluating studies of isolated factors.

In general, the agrarian aspects of mountain peoples are stressed at the expense of their urban aspects. Great attention is paid, for instance, to the transhumance of sheep and cattle between plains and mountains, little to the seasonal migrations of people between mountains and plain cities; much attention is paid to the isolation of villages, none to the corridor nature of some mountain cities and their consequent aculturation. The neglect of the functions of city types (collection-distribution-transport, health-recreation, culture, war, etc.) constitutes the book's greatest lapse in fulfilment of title.

In the treatment of mountain pathology, physical ailments are stressed, and the various forms of mental dislocation neglected. Specific effects of mountains on ethnology are treated only impressionistically in the preface and last chapter. Interesting to ecologists, however, are descriptions of functional boundaries, economic zones, straddle economies, and the democratic-socialist political climate of mountains.

The extensive bibliographies following each chapter are rendered usable by annotation; quantitative studies are made uniform by the general use of the metric system, and usable by its appended translation into the English system. The book will therefore be found of very great value not only to scientists but also to technologists, to persons engaged in snow surveying, flood and soil control, irrigation and silviculture, as well as in human eco-technical operations such as the drafting of boundaries, treaties, laws, and constitutions of Western mountain regions.

Professor Peattie's treatment of inorganic factors completes the foundation of the functional study of mountains. In spite of its neglect of volcanoes, wild animal life, and mountain cities, "Mountain Geography" is, in fact the most advanced English treatment to date of the interrelations of mountains and their organic and inorganic environments.

EDWARD F. HASKELL

GROWTH OF CONIFEROUS SEEDLINGS WITH VARIED SOIL NITROGEN AND RADIATION INTENSITIES

The importance of co-operation in ecological research is widely recognised, but it is not often that we are privileged to see such an example of it as the work on the growth of coniferous seedlings under varied conditions of soil and radiation, described by Gast in a recent publication of the Swedish Institute for Experimental Forestry.¹ The work is of exceptional interest in itself, and as a contribution by an American to the well-known series of studies on the development of conifers in raw humus, the first of which was by Hesselman and the second by Melin.²

The author covers not only his work at the Swedish Institute for Experimental Forestry near Stockholm in 1930, while he held a National Research Council Fellowship, but subsequent work on the Harvard Forest at Petersham with Mitchell, in 1931, and by himself in 1932-34, and he also utilizes results obtained by Mitchell on the Black Rock Forest at Cornwall-on-Hudson.³ He furthermore analyses data obtained by Aldrich-Blake on Corsican pine at Kennington, England.⁴

The nature of the study, and the author's attitude toward it, are indicated by a remark in the Introduction. He says: "Enough has been learned to suggest that further progress now requires the variation of two or more factors simultaneously. But if the individual effects are to be separated, in-

¹ **Gast, P. R.** 1937. Studies on the development of conifers in raw humus. III. The growth of Scots pine (*Pinus silvestris* L.) seedlings in pot cultures of different soils under varied radiation intensities. *Medd. Statens Skogsförsöksanstalt* 29 (7): 587-682.

² **Hesselman, H.** 1927. Studier över barrträdsplantans utveckling i råhumus. I. Betydelsen av kvävemobiliseringen i råhumustacket för tall-och granplantans första utveckling. (Resümee: Studien über die Entwicklung der Nadelbaumpflanze in Rohhumus. I. Die Bedeutung der Stickstoffmobilisierung in der Rohhumusdecke für die erste Entwicklung der Kiefern-und Fichtenpflanze). *Medd. Statens Skogsförsöksanstalt* 23 (6): 337-432.

Melin, E. 1927. *Idem.* II. Mykorrhizans utbildning hos tallplantan i olika råhumusformer. (Resümee: Die Ausbildung der Mykorrhiza bei der Kiefern-pflanze in verschiedenen Rohhumusformen. *Idem.* 23 (7): 433-494.

³ **Mitchell, Harold L.** 1934. Pot culture tests of forest soil fertility with observations on the effect of varied solar radiation and nutrient supply on the growth and nitrogen content of Scots and white pine seedlings. *Black Rock Forest Bull.* 5: 1-138. *Cornwall-on-Hudson, N. Y.*

—, 1936. The effect of varied solar radiation upon the growth, development and nutrient content of white pine seedlings grown under nursery conditions. *Black Rock Forest Papers* 1 (4): 16-22.

⁴ **Aldrich-Blake, R. N.** 1930. The plasticity of the root system of Corsican pine in early life. *Oxford Forest Memoir* 12; 1-64 1932.

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creased precision is necessary in the measures both of growth and of the factors conducive to growth." One of the results of these more precise measurements which will probably influence future work is the finding that "the yield formula of Mitscherlich and the compound interest formula can be used with surprising precision to relate to each other the nutrition and the cumulative dry weights of seedlings."

The base of the calculations was the "reserve dry weight" of the seeds, obtained by weighing the individual seeds and deducting the weight of the seed coat, the seed being divided into weight classes for each of which a correction factor was computed. The seedlings were grown in pots.

The principal soil condition studied was the nitrogen content. Two different methods were used. In Sweden, humus of different kinds was mixed with sand, the selection being based on Hesselman's extensive investigations of varying humus types.⁵ The nitrogen was determined by storage tests measuring the mobilization of total nitrogen both as ammonia and nitrate. The best soil, the good raw humus, showed 75.4 mg. per kg., the worst, the bad raw humus, only 1.3. On the Harvard Forest, sand was flooded with nutrient solutions of pure chemical salts, in which the nitrogen content was varied by definite amounts while the other nutrients were kept constant. Radiation was controlled by a series of screens, one of them a water screen, under each of which was placed the full series of soil conditions. Radiation was measured by pyrhelimeters, and is expressed as percentages of full sunlight, and also as kilogram calories per square centimeter (kg. cal./cm²) on a horizontal surface.

The results justify the employment of the two variables. With low radiation, the fertility of the good humus was ineffective, either in the production of dry weight, roots, or a good shoot/root ratio. All three are markedly influenced by both radiation and soil fertility. Above a certain radiation intensity the soil fertility becomes the more important.

The definite control of the nitrogen supply in the nutrient sand culture experiments brought out a number of interesting and important relationships between nitrogen supply and radiation in their influence on growth. It was found that the effect of nitrogen supply is always dominated by the level of radiation. Between nitrogen supply and dry weight there is a logarithmic: logarithmic relation. Between radiation intensity and dry weight there is a logarithmic: arithmetic relation valid under certain nutrient conditions when the measure of radiant energy is total radiation.

Comparison of the effects of increasing the nitrogen supply on the dry weight was made in such a way as to show the relative efficiency of nitrogen use by Scots pine, Corsican pine (*Pinus laricio* Poir. var. *corsicana*) and white pine (*Pinus strobus*). The Scots and Corsican pines are much more efficient than the white pine.

⁵ *Loc. cit.* footnote 2.

Examination of the internal nitrogen of the seedlings brought out further interesting relationships. In the nutrient-sand cultures, for relatively low concentrations (large concentrations were toxic), there is a linear relationship between nitrogen supply and the nitrogen content of the plant. Notwithstanding large differences in the size of plants and corresponding root systems, when the nitrogen is supplied in artificial cultures the internal nitrogen content of plants grown under widely differing radiation are very close. It appears that an internal nitrogen content of about three per cent of the dry weight is most favorable for the maximum yield of Scots white and Corsican pines in the seedling stage.

In the humus-sand cultures the nitrogen supply is complex, as it is under natural conditions in the forest, and the nitrogen mobilization tests do not permit the measurement of the amounts currently available as in the nutrient-sand cultures. This difficulty was largely overcome by determining the internal nitrogen, and comparing the nitrogen uptake at different radiation intensities. It was found that, in contrast with the artificial nutrient cultures, the nitrogen uptake on the good raw humus increases greatly as the size of the plant is increased by more intense radiation. This difference illustrates the need of comparing results from artificial nutrient cultures with those from natural soil conditions, and the value of close co-ordination between laboratory and field experiments. Such co-ordination is one of the strong points of Swedish forestry research.

A series of three very ingenious three-dimensional charts summarises the relation of radiation and nitrogen uptake to three important aspects of growth, namely dry weight, development of long lateral roots, and shoot/root ratio. They show that only when the radiation approximates 20 per cent of full sunlight (about 5 to 7 kg. cal./cm² from June 1st to September 1st) does the nitrogen supply become important. Only with 18 or more kg. cal./cm² for the 3 summer months can Scots pine use to advantage the nitrogen in rapidly mobilizing raw humus.

The experiments incidentally clear up the question of the relative influence of light versus moisture on the development of seedlings under a forest canopy, which has caused so much discussion since trenching experiments, by removing root competition and increasing the available moisture, have given rise to the opinion that the poor development of seedlings in the shade was due to lack of moisture rather than to lack of light. The limit of 20 per cent of full sunlight above-mentioned for Scots pine applies when all other factors such as moisture and nutrients are favorable. The poor development of seedlings in the shade is, therefore, definitely attributable to deficient radiation. This does not mean that moisture is not often insufficient, but that, as other experiments have shown,⁶ ample moisture does not make up for deficient radiation.

⁶ Moore, Barrington. 1926. Influence of certain soil and light conditions on the establishment of reproduction in north-eastern conifers. *Ecology* 7: 191-220.

The work is in English, with a Swedish summary by Hesselman, and the typography is of the usual high standard characteristic of the publication of the Swedish Institute for Experimental Forestry. It has been made readily available to American readers by being reprinted for the Harvard Forest.

BARRINGTON MOORE

CORFE,
TAUNTON,
ENGLAND

THE VEGETATION OF PETÉN

During the past two decades a couple of very different factors have focused attention on the Yucatan region. Archeologists have become interested in the ancient Mayan civilization and huge exports of chicle, obtained from the zapote tree, *Achras zapota*, have gone to the manufacturers of chewing gum. Both have resulted in an increasing knowledge of the vegetation of the region. This journal has previously reviewed a preliminary paper by Lundell¹ and is now glad to notice a more detailed study of northern² Guatemala by the same investigator.

Petén is the most northerly province of Guatemala and is relatively isolated by mountains on the south, east and west, the portion studied being a dissected plateau with an elevation of some 400 meters. Precipitation averages about 1760 mm. annually, with a dry season from November to May. Average monthly temperatures range from 20.7° C. for February to 29.5° C. for April, with extremes of 14.4° and 38.9°. The upland soils are well drained, immature, calcaceous clays (Rendzinas) thinly spread over limestone. On the poorly drained lowlands deep acid clays are found.

The Mayan system of agriculture, or *milpa*, which consists of cutting down the forest, burning the slash at the end of the dry season, raising two crops of maize, beans and gourds and then abandoning the area for a new one, has been practiced by a considerable population for many centuries. This doubtless has had an influence on the vegetation in producing a forest more scrubby than the luxuriant broad-leaved climax type characteristic of undisturbed portions of the uplands. This is a quasi-rain forest of several hundred tree species widely and evenly distributed. Among the tree giants, of which there are two or three per acre, are species of *Swietenia*, *Ficus* and *Brosimum* together with *Achras zapota*. Lianas are conspicuous including spiny palms of the genus *Desmoncus* and woody Bignoniaceae and Malpighiaceae. Root-climbing cacti form immense tangled masses. Three major associations dominate the formation characterized by *Brosimum alicastrum*, *Swietenia macrophylla* and *Achras zapota* respectively. Three-fourths of the upland forest of northern Petén belongs to this last association.

¹ ECOLOGY 16: 262-263. 1935.

² Lundell, Cyrus L. 1937. The vegetation of Petén. *Carn. Inst. Wash. Publ.* 478. 1-244. 39 pl.

The influence of the *milpa* agriculture is also seen in a great variety of successional stages which are outlined.

In central Guatemala the forest passes into a savanna region in which the dry season from February to May seems to be more pronounced, although meteorological data are very scanty. This central area, which is very fertile, seems to have been more densely populated by the Maya and their successors. During the dry season fires are abundant and destructive and these together with cultivation seem adequate causes for the absence of forests. The grassland flora seems to be that common to many areas of Central America. The region is largely covered with perennial grasses about a meter or less in height. Various associations are recognized, their vegetation described and the flora listed.

Perhaps the most valuable part of the investigation consists of the extensive collections represented by long annotated lists. Plates consisting of photographic illustrations and diagrammatic cross sections make the descriptions more intelligible. An appendix contains descriptions of several new species and an extensive bibliography is provided.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

SOME NEW BOOKS

Among the textbooks that have appeared recently are several that seem to deserve the notice of ecologists although they do not directly contribute to the development of this particular branch of science.

A new textbook in general biology by Kenoyer and Goddard¹ seems to possess several points that should recommend it. It places much emphasis on the ecological relationship existing between plants, animals and man, it contains an abundance of material calling for field study and includes a great number of specific types from the great animal and plant groups which are necessary to furnish an adequate basis for the intelligent grasp of fundamental biological concepts.

A second edition of *Plants Useful to Man*² indicates the acceptance by the public of this useful book. The authors have made several minor improvements in the illustrations and in the text but the original plan remains unchanged.

A new book on soil science³ presents the principles of the modern aspects of this science in terms easily understood by intelligent laymen. It is evidently intended for a textbook for students in agriculture and forestry for at least three-fourths of the volume is devoted to the economic application of

¹ Kenoyer, Leslie A. and Henry N. Goddard. 1937. *General Biology*. XXIII + 630 pp. 367 fig. *Harper and Brothers*. New York. \$3.50.

² Robbins, Wilfred W. and Francis Ramaley. 1937. *Plants Useful to Man*. Second Edition. VII + 422 pp. 229 fig. *P. Blakiston's Son & Co. Philadelphia*.

³ Weir, Wilbert W. 1936. *Soil Science; Its Principles and Practice*. IX + 615 pp. 134 fig. *J. B. Lippincot Company. Philadelphia*. \$3.50.

the principles involved. The ecologist will be interested in the non-technical presentation of the principles of pedology and in the elucidation of the modern classification of soils. The relationship of natural vegetation to soil formation is emphasized and extensive citations of more technical literature are given.

As gardening involves the principles of ecology it may follow that some ecologists may be interested in a new encyclopedic treatment of all phases of garden making. The author ⁴ trained at the Royal Botanic Gardens, Kew, and now at the Brooklyn Botanic Gardens is familiar with the scientific as well as the practical aspects of plant growth. The book is readable, it seems to be scientifically accurate, the material is accessible and well indexed while the illustrations are numerous and excellent.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

LIFE HISTORY OF THE SONG SPARROW ¹

Mrs. Nice's studies on the natural history of the song sparrow were well known among ornithologists before the publication of the present extensive report. Her work deserves attention also from ecologists who are interested in a detailed analysis of the "co-actions," "interactions" and "reactions" of a single conspicuous species viewed against a biotic background which she outlines and partially sketches in.

The report is fragmented into numerous short chapters, each with an elaborate summary, and invites the browsing type of reading. Since many ecologists will come to this work without previous introduction it may be well for them to read the initial section of the appendix first.

The studies have the strength and some of the weakness of having been made by a so-called amateur, who is a naturalist with much experience in this and other fields of investigation. From a considerable experience with the writings of budding and mature professionals, it seems to me that only rarely does one find in so-called professional work the evident love of the subject matter in all its details which appears here. The observations at seasons other than late summer are generous in quantity and detailed and exact in quality. The birds are followed as individuals, especially during the establishment of spring territories and the nesting activities of spring and early summer. There was no thorough-going study of the birds during the late summer season.

Among the many important subjects on which pertinent data are presented, there is a discussion of the relative rôle of temperature and other factors, including length of day, as regards various aspects of seasonal

⁴ Free, Montague. 1937. Gardening; a Complete Guide to Garden Making. XVI + 550 pp. 198 fig. *Harcourt, Brace and Company. New York.* \$3.50.

¹ Nice, Margaret Morse. 1937. Studies in the Life History of the Song Sparrow. I. A population study of the Song Sparrow. *Trans. Linnaean Soc. New York* 4: 1-247.

behavior. The conclusion reached is that temperature seems to be more important than much recent work would indicate. As regards the relative importance of light and temperature Mrs. Nice finds (p. 67) that the amount of singing correlates very well with the average temperature of January and February, but does not correlate with the percentage of sunshine. The starting of laying is also correlated with temperature sufficiently for formulae to be suggested to express the relationship.

Neither the author nor the reviewer are interested in minimizing the effect of cyclic changes in length of day. We are both concerned to know the extent and importance of the influence of light. In this connection, it is interesting to note (p. 110) that individual female song sparrows normally lay 4 sets of eggs in a season. These are distributed from about mid-April until mid-August, with intervals of about a month between sets. This is of interest to the student of the effect of length of day because the laying begins when the days are fairly long and are still lengthening, and continues past the mid-summer solstice well into the period of decreasing length of days. It is also important to remember that those producing the late sets were not young birds producing their first eggs, as has been suggested by some students of the influence of light who have been concerned about this particular phenomenon.

The population trends of these song sparrows do not support the sun-spot cycle theory of abundance. In this connection, Mrs. Nice states (p. 207) that she has "one chief criticism of theories on population questions . . . they all present too much theory based on too few facts. . . ." This is not so much the fault of the theorists, she concludes, "as that of naturalists the world over in not giving them data on which to work. We need a great body of facts intelligently and conscientiously collected before we can safely launch into elaborate theories." This statement might have been a commonplace remark a few years ago, but to those of us who live in the shadow of well publicized efforts to establish a neo-scholastic philosophy largely divorced from modern scientific evidence, it seems a wholesome and timely note. The statement is also worthy of inclusion in this review since it summarizes accurately the apparent motivation and the strength of the present study.

W. C. ALLEE

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ECOLOGICAL ANIMAL GEOGRAPHY¹

This book, which is an English translation of Hesse's *Tiergeographie auf oekologischer Grundlage* with considerable modification and revision by Allee and Schmidt, is a welcome addition to the growing list of standard treatises on Ecology. Ecology is incorporated as the influence of the environmental factors separately and together on the distribution of animals. Even the treatment of isolating factors as ecological influences upon evolution is presented

¹ Hesse, R., W. C. Allee and K. P. Schmidt. 1937. *Ecological Animal Geography*. John Wiley & Sons, Inc., New York. 597 + xiv pp., 135 figs. \$6.00.

in a balanced perspective, although the authors emphasize the need for another summarizing book which should deal primarily with historical animal geography with particular attention to animal phylogeny.

Professor Hesse's splendid summary of the European literature on the subject is augmented and modified through the inclusion of many American studies. It is fortunate that two American workers of such diverse viewpoint and experience as Allee with his physiological leanings and Schmidt with his taxonomic interests should find Hesse's volume so inspiring that they were able to undertake a cooperative revision. Such a book is far more likely to avoid personal bias and overemphasis and it thus is the first book undertaking to cover a wide ecological field which the reviewer finds well balanced and without obvious misinterpretations or serious gaps in the subject matter. It is possible to find a few conclusions with which the reviewer is not in accord, and here and there one might find better examples to illustrate certain principles, but a review that attempts to be as well balanced as the book cannot mention these minor points without emphasizing unessentials out of proportion to the whole.

The organization of the subject matter is primarily on the basis of the marine, limnological and terrestrial communities and these in turn are discussed with reference to the principle environmental factors and their influence. The ecological principle under discussion is illustrated by a wide variety of animals which show parallel physiological or structural adaptation. The theory of adaptive adjustment is carefully and broadly treated throughout the book in a manner that convinces the reviewer that the past split in the ranks of ecologists over this question is being satisfactorily healed through more mature consideration of the wealth of factual evidence.

It is with pleasure that we find the book devoting equal consideration to the ocean, fresh water and land communities. Research students are forced into specialties in order to avoid superficiality, but principles become stronger when shown as applicable in diverse environments. It is hoped that this book will tend to bring the oceanographer, limnologist and terrestrial ecologist into more sympathetic relationship.

The title of the book emphasizes the hybrid nature of the subject matter. It would seem that in this case hybrid origin lends vigor and vitality to the offspring rather than sterility due to fundamental lack of harmonic balance of the organismal determiners. Ecology is a science which of necessity must exert its influence upon many other disciplines. It is true that we need to have ecological principles carefully formulated into a coherent viewpoint, but like the field of embryology, ecology merges into other fields without perceptible lines of demarkation. The wide influence of the ecological attitude in biological and sociological fields is merely a manifestation of a wholistic tendency. This cooperative study by Hesse, Allee and Schmidt is an excellent example of the synthetic effect of the science of ecology.

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NOTES AND COMMENT

PRODUCTIVITY OF A LAND SNAIL, *POLYGYRA THYROIDES* (SAY) ¹

In determining the general biological importance of an organism in any habitat, quantitative observations on distribution and relative abundance are necessary. In a prolonged field study of *Polygyra thyroides* the writer became interested in the yield of this snail as an index to its importance, especially in food relations.

On September 12, 1935, a field trip was made to the flood plains of the Sangamon River near White Heath, Illinois, for the purpose of securing data regarding the numbers that comprise the population of *Polygyra thyroides* in a definite area. The entire day was spent in making counts in measured areas. With the aid of an assistant who kept records of the count, eleven representative one square meter areas in the flood plain were surveyed. Counts were made of all the living *P. thyroides* found in each square meter and were recorded with notes of other macroscopic animals present. For the purpose of this study, however, no attention will be given to the other animals that were found associated with *P. thyroides*.

As each area represents a modification of a flood plain habitat which erroneously might be thought of as of uniform composition throughout, it is believed that a short description of the various stations selected to represent all the conditions that obtain should be included in this report.

(1) The first square meter count was made at the forest edge on a square meter approximately a meter in from the margin. Ground cover scanty but plenty of shrubs to shade the area. Two *P. thyroides*.

(2) Five meters from the forest edge. Shrubs taller and ground cover more scanty than in the first. Three *P. thyroides* (two adults and one juvenile).

(3) Ten meters in from the edge. Ground cover still scanty, shrubs less abundant and trees larger. Two specimens.

(4) Fifteen meters in from the edge. Beginning of typical forest floor condition. Shrubs peculiar to forest edge lacking. Ground cover of leaf mould and small grasses. Seven specimens.

(5) Well within flood plain forest, approximately 30 meters from edge. Ground level somewhat lower than general level of flood plain. Woods nettle, growing profusely, about one-fourth defoliated by *P. thyroides*. Area well shaded by trees. Ground cover scarce. Three snails.

(6) A low moist area ten meters from bank of river. No *P. thyroides*.

(7) Well within forest about 30 meters from stream. Nettles composed herb layer and leaf mould covered ground. Four young *P. thyroides*.

(8) A low plot near river. Some nettles were present but very little ground cover. Two *P. thyroides*, one clinging to the nettles.

(9) North end of collecting site not far from low bluffs that approach close to river at that point. Perhaps the highest part of the flood plain. A very heavy ground cover of leaf mould, flood debris and fine wood brush. Fifteen adults and juvenile specimens.

(10) Nearer the bluff than the one just described and the same general appearance as to ground cover and shrubs. Ten specimens.

¹ Contributions from the Zoological Laboratory of the University of Illinois, No. 511. A section of the doctoral dissertation by the late Mr. Foster, edited by H. J. Van Cleave, under whose direction the thesis was written.

(11) A typical land snail habitat. Forest floor was covered with a partially decomposed deposit of flood debris caught by a rotting log. Nettles were growing up through this cover and again gave evidence of the snails using the succulent leaves as food. Twenty-one specimens of *P. thyroides*.

It is estimated that the eleven sites selected for this study portrayed the conditions existing over more than one half the collecting area. There are many bare spots in the area (such as the sites of temporary ponds, old channels, etc.) where there is neither ground cover nor growing plants. Barren ground offers no protection to land snails so none are found there.

It was found by weighing the adult snails in the laboratory that the average weight of the living snail is approximately 3 grams. An empty shell of average size weighs 0.5 grams. Deducting this weight of the shell from the total weight of the snail it is found that the average *P. thyroides* offers 2.5 grams of living tissue available as food for other animals.

An average of the eleven counts made in this survey shows that there are six and one-third *P. thyroides* per square meter on the area of the flood plain available as habitat for this species of snail. This amounts to 25,630 snails per acre, weighing 76.9 kilograms, or 169.18 pounds. Deducting the weight of the shells there are 140.96 pounds per acre of living snail tissue of this one species in the flood plain habitat. This is a conservative estimate of the amount of snail tissue present in the greater portion of the flood plain habitat under normal conditions when the snails are well established. Note that this is not annual production, but amount of one species present at one time.

These figures probably denote the maximum production when the largest numbers prevail. However, counts made in three successive months based on just one square meter gave for October 14, 6 individuals; November 16, 7 individuals; and December 14, 9 individuals. Thus it seems that for the fall season fairly constant numbers are maintained. It is thought by the writer that the activity of natural enemies during the winter months reduces the snail population so that these figures would be noticeably altered by spring. No counts have been made to verify this view. Areas greater than a square meter have been diligently searched in sites where the short-tailed shrew (*Blarina brevicauda*) has been active and not a living adult snail could be found.

Figures obtained from Dr. D. H. Thompson, of the Illinois State Natural History Survey over a period of years in his study of fish population and annual production show that the flood-plain lakes of the Illinois River produce the greatest amount of fish weight per acre of any Illinois waters. The average yield in any one year for these lakes is 100 to 150 pounds per acre. Other Illinois streams and lakes show yields varying from 25 to 75 pounds per acre.

It can be seen from this study that *P. thyroides* is no insignificant link in the food chains of the area. These figures of weight per acre, although not as great as reported for some animals, show that this species of snail certainly must play an important part in the "balance of life" of the flood plain habitat. There are numerous observations on the use of *P. thyroides* as food by the short-tailed shrew. Incidental experiments carried out in the present study indicate that the material reduction in population of *P. thyroides* through the winter is due largely to predatory animals of which the short-tailed shrew is the most important. Climatic factors seemed to have relatively unimportant effect in reducing populations under conditions of nature where predators were excluded.

T. DALE FOSTER

UNIVERSITY OF ILLINOIS

AGROPYRON SMITHII

Floods and dust storms plus current articles in newspapers and magazines are doing much to make this country conservation minded. A new measuring stick—"conservation value"—is being used when choosing cultivated or native plants for erosion control purposes.

Plants which produce large quantities of viable seed, especially under rather adverse conditions, and which are adapted to a wide range of soil and moisture conditions are especially desirable for soil conservation work. Other factors which would be helpful are high palatability, vigorous seedling qualities, ability to withstand sand blasting and rapid root and stem development.

One native species which has a large number of these conservation value traits, especially for the central and northern Great Plains is *Agropyron smithii* (Rydb.). The most widely used common name of this species is western wheatgrass.

Western wheatgrass is generally conceded to be a consociation in the shortgrass plains, especially on certain "hard" soils particularly those derived from the Pierre shale. There seems to be differences of opinion, however, concerning this question among ecologists. It is the writer's observation, nevertheless, that this general relationship holds throughout most of the high plains section of Western Nebraska and the northern Great Plains area.

Undoubtedly this grass is one of the most promising species to use in the general region of the Great Plains for erosion control work. It has a heavy mat-like root system, which penetrates six feet or more in depth. It seems to thrive under a wide range of conditions and is well adapted to resist drought, chiefly by its ability to revive after desiccation. It spreads rapidly by rhizomes as well as by seed.

Farmers have reported that when a sod composed of western wheatgrass and short grass is broken or disked heavily and allowed to remain without further cultivation the growth of the wheatgrass is greatly increased. The wheatgrass plants are not killed by this process nor do they seem to suffer as much damage as the short grasses and there is a more abundant water supply available to them as a result of the destruction of the short grasses.

In Kimball county, Nebraska, cattle men considered western wheatgrass hay one of the best winter feeds. Yields of from one-half to two tons of western wheatgrass hay per acre in the fall of 1935¹ were reported.

Western wheatgrass is one of the first perennial grasses to make its appearance on abandoned fields. From a study² of succession on abandoned fields in Kimball county, Nebraska, it was found that on fields abandoned for six years, this species comprised 37 per cent of the total vegetation.

Since the interest shown by the Government in securing seed of native grass species, seed of western wheatgrass is available from most seed houses in the middle west.

Western wheatgrass fits well into the general farming enterprise since the same machinery used for small grains can be used for it. If it is raised for seed production the seed can be harvested with a combine or cut with a mower or binder and then threshed. If the combine is used most of the plant is left in the field for grazing and soil protection.

Ordinary grain drills can be used for sowing the seed. It is felt that the seed should be sown as shallow as conditions will permit, from .125 to .5 inch being recommended. Late fall or early spring seeding is no doubt the best.

B. IRA JUDD

MANDAN, NORTH DAKOTA

¹ An especially favorable year for grass production in this vicinity.

² Unpublished manuscript by the author.

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